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JOURNAL OF PALEONTOLOGY

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ADDITIONS TO THE WHITNEYAN FAUNA OF SOUTH DAKOTA

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ABSTRACT—A new species of insectivore, *Apternodus bicuspis* and a new species of artiodactyl, *Archaeotherium* (*Pelonax*) *lemleyi* are described from the Whitneyan member of the Brule formation in South Dakota. The presence of the creodont, *Hyaenodon* is recorded for the first time from this horizon in North America.

INTRODUCTION

DESPITE the great numbers of fossil remains that have been recovered from the White River Badlands, there are additions to the faunas recorded each year. Hayden, in 1869, direly predicted that there would be no more profitable collections made from these beds, but today there seems to be no end to the number of specimens that may be collected each season through diligent search. Nevertheless, a survey shows that there are still a great number of blanks in the faunas from the *Leptauchenia* clays and the *Protoceras* channels. This lack of information is a reflection of the difficulties presented to the collector by the isolated occurrence of these exposures and the rugged topography encountered when the exposures are prospected. As a result, a detailed exploration of the Whitney member of the Brule formation has been neglected and collectors have, in general, confined their efforts to the more profitable Orella member and the Chadron formation.

The material described below was collected by personnel from the South Dakota School of Mines and Technology Museum of Geology. The figures were prepared by Mr. Leslie Davis.

DESCRIPTION OF MATERIAL

INSECTIVORA

SOLENODONTIDAE

APTERNODUS BICUSPIS* Macdonald, n. sp.

Type.—Partial cranium, S. D. S. M. Mus. no. 4048. A slightly crushed partial cranium with unworn canine, P^{2-3}, alveoli of P^4 and M^{1-2}.

Type locality.—*Protoceras* channel sandstone, seven miles east of Rockyford, Shannon County, South Dakota.

Fauna.—White River.

Age.—Whitneyan. Upper Oligocene.

Diagnosis.—P^3 with anterior cingular cusp reduced; principal cusp large; conical; posterior lingual cusp joined to principal cusp by trenchant ridge; internal cusp conical, one half size of principal cusp. P^2 nearly circular; close to P^3. Canine greatly reduced, relatively shorter anteroposteriorly than in other species.

Description.—P^4 and M^{1-2} represented by roots or alveoli. P^3 with anterior cingular cusp reduced to small tubercle on cingulum; principal cusp large, conical with small depressed area linguad to anterior cingular

* *Bicuspis*, in reference to the twin cusps of P^3.

cusp; posterior cingular cusp small, connected to principal cusp by trenchant diagonal crest; lingual cusp enlarged, conical, at anterolingual corner of tooth, separated from principal cusp by deep V-shaped valley which flattens posteriorly into level-floored open valley; posterolingual corner expands into incipient cusp, with faint ridge running down posterior side of lingual cusp to summit of incipient cusp and bifurcating, one branch forms posterior margin of U-shaped valley, the other runs to cingulum near posterolingual corner. Cingulum well developed on posterior side, broken at posterolabial corner, continuous on labial side and anterior side to point opposite junction of principal and lingual cusps. P^2 close to P^3, conical, expanded slightly posteriorly and lingually; cingulum continuous, most prominent on posterior moiety. Canine separated from P^2 by small diastema, subtriangular with flattened crest running posterolingually from cusp.

Discussion.—Apternodus bicuspis shows a general increase in size over the older species. P^3 has moved somewhat labially and become enlarged into a more prominent and effective part of the dental battery. It has rotated slightly so that its transverse axis is perpendicular to the long axis of the skull. The enlargement of the lingual cusp is a progressive feature which offsets the great reduction of the anterolabial cingular cusp. A relative shortening of the rostrum has closed the diastema between the P^2 and P^3. P^2 has become less elongate and more conical. The diastema between the canine and P^2 is greatly reduced over the condition found in *A. gregoryi* Schlaikjer (1933) and *A. brevirostris* Schlaikjer (1934). The canine has become reduced until it is but slightly larger than P^2 and is apparently not only premolariform in shape but also in function. A comparison cannot be made with *A. mediaevus* Matthew (1910) and *A. altitalonidus* Clark (M.S. in Scott and Jepsen, 1936) as these two species are based on lower jaws.

TABLE 1—MEASUREMENTS IN MILLIMETERS OF SPECIES OF *Apternodus*

	A. bicuspis	*A. gregoryi*	*A. brevirostris*
Cranium, height above alveolus for M^1	14.5	—	12.6
Cranium, length from antorbital ridge to occipital condyle	46.0	32.1	33.0
Tooth row, length from canine to P^4 inclusive of alveoli	14.4	—	8.6
Canine, greatest anteroposterior diameter	2.8	—	2.2
Canine, greatest transverse diameter	2.3	—	1.5
P^2, greatest anteroposterior diameter	2.3		
P^2, greatest transverse diameter	2.5		
P^3, greatest anteroposterior diameter	3.8		
P^3, greatest transverse diameter	5.2		

CARNIVORA
HYAENODONTIDAE
HYAENODON cf. CRUENTUS Leidy

While prospecting the *Leptauchenia* clays, near Oelrichs, South Dakota during the 1932 field season, Mr. James Bump and Mr. Robert Hernon of the School of Mines were fortunate enough to find and collect five skulls of *Hyaenodon*. This, I believe, constitutes the first post-Orellan record of creodonts in North America.

Three of these skulls are from adults and two are from juveniles. Unfortunately, much of the material from the upper horizons in this region is badly crushed and only partially preserved so these specimens are somewhat distorted and incomplete. One juvenile cranium (no. 328) is very fragmentary and the other (no. 3211) consists of the rostrum only, with the deciduous canine, P^1 and dP^2–M^1. P^4 has been exposed by removing the outer surface of the maxillary. Among the adult specimens there is a young individual (no. 323) with P^2–M^2 on one side and P^3–M^2 on the other and P_4–M_3 in each mandibular ramus. The other fairly complete skull (no. 3268) is very badly crushed

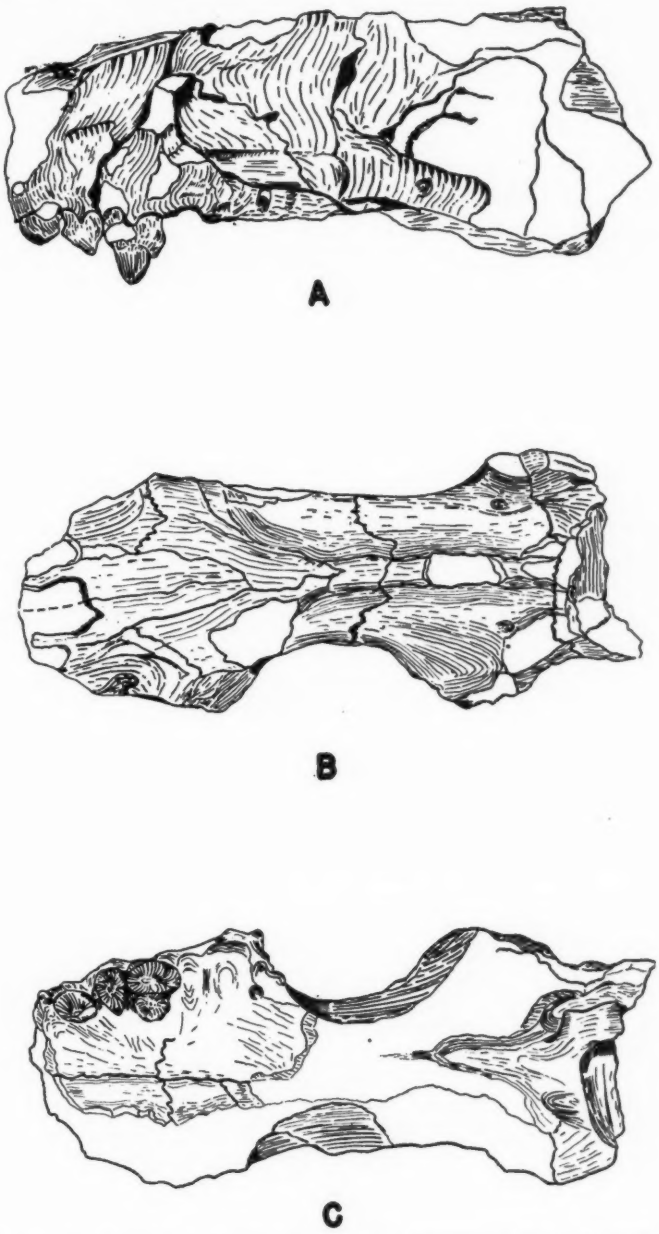

FIG. 1—*Apternodus bicuspis* n. sp. (type specimen), fragmentary cranium; *a*. lateral view; *b*. dorsal view; *c*. palatal view. No. 4048. ×2.

and poorly preserved but contains right P^2–P^4, left P^{1-3}; both rami contain the roots of I_{1-3}, the canines, the alveoli of P_{1-2}, moderately worn P_{3-4}, the roots of M_1 and heavily worn M_{2-3}. The last specimen (no. 326) consists of the rostrum only and contains the roots of I^2–P^4 and heavily worn P^4–M^2.

Specific determination among the medium sized Oligocene Hyaenodons does not seem

to be entirely satisfactory due to the great range of variation shown by the described individuals. A comparison of dental measurements indicates that these specimens seem to fit within the limits assigned to *Hyaenodon cruentus* Leidy (1853). It is not felt that this is an adequate means of determination, but on the basis of the character of the material at hand these individuals are tentatively assigned to that species.

Fauna.—White River.

Age.—Whitneyan. Upper Oligocene.

Diagnosis.—Posterior tubercle long, round in cross section; mental tubercle massive, tapering proximo-distally; P_2 and P_3 separated by diastema.

Description.—M_3 subequal to M_1; transverse diameter one-fourth less than anteroposterior diameter; undeveloped hypoconulid; hypoconid and entoconid not as tall as protoconid and metaconid, hypoconid and protoconid partially separated by labial V-shaped valley, entoconid and metaconid separated by large basin; metaconid taller than other cusps, faint anterior cingulum partially destroyed by appression of M_2. M_2 similar to M_3; posterior face concave due to appression of M_3, posterior moiety slightly narrower than anterior. M_1 similar to other molars; anterior moiety slightly narrower than posterior; anterior cingulum well developed. P_4 elongate; well developed basined heel; principal cusp asymmetrical with basined steeply sloping posterior edge, gently sloping anterior edge; posterior and anterior cingula well developed. P_3 massive, conical, base of crown opposite apex of P_4, anterior edge convex, posterior edge

TABLE 2—MEASUREMENTS IN MILLIMETERS OF TEETH IN SPECIMENS OF *Hyaenodon* CF. *cruentus* LEIDY

	323		326	3268	
	left	right	left	left	right
M^2, greatest anteroposterior diameter	21.5	21.5	24.2		
M^2, greatest transverse diameter	13.0 ap.	13.4	12.5 ap.		
M^1, greatest anteroposterior diameter	16.0	17.2			
M^1, greatest transverse diameter	8.7	8.7			
P^4, greatest anteroposterior diameter	14.2	14.8	15.0 ap.		17.3
P^4, greatest transverse diameter	12.6	12.7	12.0		13.5
P^3, greatest anteroposterior diameter		12.8		17.5	17.6
P^3, greatest transverse diameter		8.8		10.3	10.3
P^2, greatest anteroposterior diameter				15.1	15.2
P^2, greatest transverse diameter				8.0	8.3
M_3, greatest anteroposterior diameter	20.5	20.2		21.2	
M_3, greatest transverse diameter	9.8	10.2		10.2	
M_2, greatest anteroposterior diameter	12.7 ap.			14.0 ap.	
M_2, greatest transverse diameter	7.2			6.7 ap.	
M_1, greatest anteroposterior diameter	10.8	10.6			
M_1, greatest transverse diameter	5.7	5.8			
P_4, greatest anteroposterior diameter	15.5	15.5		17.7 ap.	17.6
P_4, greatest transverse diameter	8.4	8.7		8.8	10.0
P_3, greatest anteroposterior diameter				16.0	15.5
P_3, greatest transverse diameter				8.5	8.3

ARTIODACTYLA
ENTELODONTIDAE
ARCHAEOTHERIUM (PELONAX) LEMLEYI* Macdonald, n. sp.

Type.—Pair of mandibles, S. D. S. M. Mus. no. 2423. Mandibular rami lacking posterior portion, with right P_3–M_1, alveoli of canine and P_{1-2} and left P_2–M_3, alveoli of P_1 and canine.

Referred material.—Rostrum, S. D. S. M. Mus. no. 4366. Rostrum with right I^3–M^3, alveolus of I^2, left P^1, P^3–M^1 and alveolus of P^2.

Type locality.—*Protoceras* channel sandstones, 1½ miles NW of Cedar Pass, Jackson County, South Dakota.

* In honor of Dr. Ray E. Lemley, M.D

slightly ridged and convex. P_2 separated from P_3 by diastema, broken, slightly smaller than P_3. P_1 separated from P_2 by diastema, roots only, roots closely appressed. Canine separated from P_1 by short diastema, massive, broken root and alveolus only. Mandibular rami very deep and massive, slightly deeper below M_3 than below diastema between P_{2-3}. Posterior tubercle long with rounded cross section, centered below posterior root of M_1, deflected laterally. Mental tubercle rounded in outline, thickened anteriorly and distally, tapering posteriorly to thin edge, concave laterally, directed anteriorly and laterally, does not extend beyond alveoli for canines.

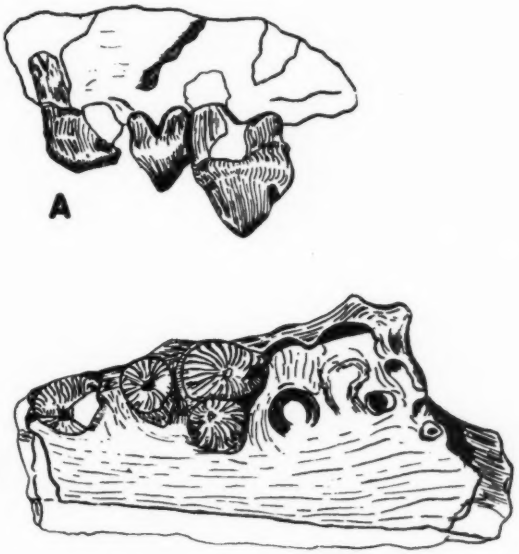

FIG. 2—*Apternodus bicuspis* n. sp. (type specimen), dentition; *a*. labial view; *b*. occlusal view. No. 4048. ×3.

Referred rostrum and upper dentition.—M^3 slightly tapered posteriorly; paracone most prominent cusp, metacone broken, partially separated from hypocone by flat, triangular shaped valley; no metaconule; protocone partially separated from hypocone by V-shaped valley, closely connected to protoconule; shallow, smooth floored basin separates four principal cups; poorly developed cingulum extends from posterolabial corner of hypocone around metacone to posterolabial corner of paracone, well developed on anterior side, with small parastyle at anterolabial corner, deep groove between base of protocone and cingulum on anterolingual corner, small segment connects protocone and hypocone. M^2 subrectangular, greatest anteroposterior diameter near labial edge; paracone and metacone subequal; hypocone closely appressed to metaconule, separated from protocone by V-shaped valley; protocone closely appressed to protoconule; cingulum forms wide posterior shelf between hypocone and posterolabial corner, faintly indicated labially between metacone and paracone, developed as shelf on anterior border with valley separating it from anterolingual corner of base of protocone, a small segment joins the protocone and hypocone. M^1 similar to M^2. P^4 bicuspid, labial cusp taller than lingual cusp, subequal in diameter; labial cusp with flattened ridges extending from apex to base on anterior and posterior faces; lingual cusp with ridge on posterior face running from apex to base near junction with protocone; cingulum well developed around posterior lingual quarter of lingual cusp, reduced on posterior side of labial cusp, well developed on anterior face from

anterolabial corner of labial cusp to midpoint on lingual cusp. P^3 slightly taller than posterior teeth; massive single cusp with concave posterior border flattened on posterolingual surface; cingulum interrupted, most heavily developed on posterior only; oviform in cross-section. I^3 separated from canine by diastema; large simple cone. I^2 root only, slightly smaller than I^3. Rostrum crushed laterally; tips of nasals and premaxillaries broken away; infraorbital foramen above diastema between P^{2-3}.

TABLE 3—MEASUREMENTS IN MILLIMETERS OF *Archaeotherium* (*Pelonax*) *lemleyi* COMPARED WITH OTHER SPECIES

	*A. potens**	*A. ramosus*†	*A. lemleyi*
M_3, greatest anteroposterior diameter	37.2		37.3
M_3, greatest transverse diameter	27.9	32	29.8
M_2, greatest anteroposterior diameter	36.1	38	37.6
M_2, greatest transverse diameter	29.4	35	30.4
M_1, greatest anteroposterior diameter	33.6	30	33.8
M_1, greatest transverse diameter	24.8	27	27.6
P_4, anteroposterior diameter alveolus	41.9		39.3
P_4, greatest transverse diameter	23.2		23.5
P_3, anteroposterior diameter alveoli	57.0	59	52.8
P_2, anteroposterior diameter alveoli	30.0	37.0	47.6
Diastema, P_1–P_2	32.0		26.2
P_1, anteroposterior diameter alveoli	28.0	37.5	23.5 ap.
Diastema, canine–P_1	9.0		—
Mandible, depth between P_{2-3}	95.0		106.2
Mandible, depth between M_{1-2}	111.0		128.0 ap.
M^3, greatest anteroposterior diameter			37.1
M^3, greatest transverse diameter			38.7
M^2, greatest anteroposterior diameter			40.5
M^2, greatest transverse diameter			42.3
M^1, greatest anteroposterior diameter			34.5
M^1, greatest transverse diameter			37.7
P^4, greatest anteroposterior diameter			27.5
P^4, greatest transverse diameter			34.5
P^3, greatest anteroposterior diameter on enamel			36.0
P^3, greatest transverse diameter			25.0
P^2, anteroposterior diameter of alveoli			40.0
P^1, anteroposterior diameter of alveoli			32.0
Canine, greatest anteroposterior diameter			49.7
Canine, greatest transverse diameter			37.0
I^3, greatest diameter			24.0
Diastema, P^{2-3}			20.8
Diastema, P^{1-2}			61.3
Diastema, canine–P^1			23.0
Diastema, I^1–canine			25.5
M^{1-3}, total length			114.4

* Courtesy of Joseph T. Gregory.
† After Scott & Jepsen, 1940.

moiety and anterolingual surface. P^2 separated from P^3 by diastema; two diverging roots, smaller than P^3. P^1 separated from P^2 by long diastema; two roots closely appressed; relatively greater anteroposterior diameter than P^2; long axis oblique to tooth row. Canine separated from P^1 by short diastema; massive long recurved tusk; apex recurved to point nearly opposite apex of P^1; enamel on distal half of crown

Discussion.—The characteristic features of the subgenus *Pelonax* are the great size of the mental tubercle and the great depth of the mandible. Cope (1874) established *Pelonax ramosus* on the shape, size and position of the tubercles, the separation of the first and second premolars by a diastema, the single rooted character of these teeth, the low cusps on the molars and the small two lobed form of the last lower molar.

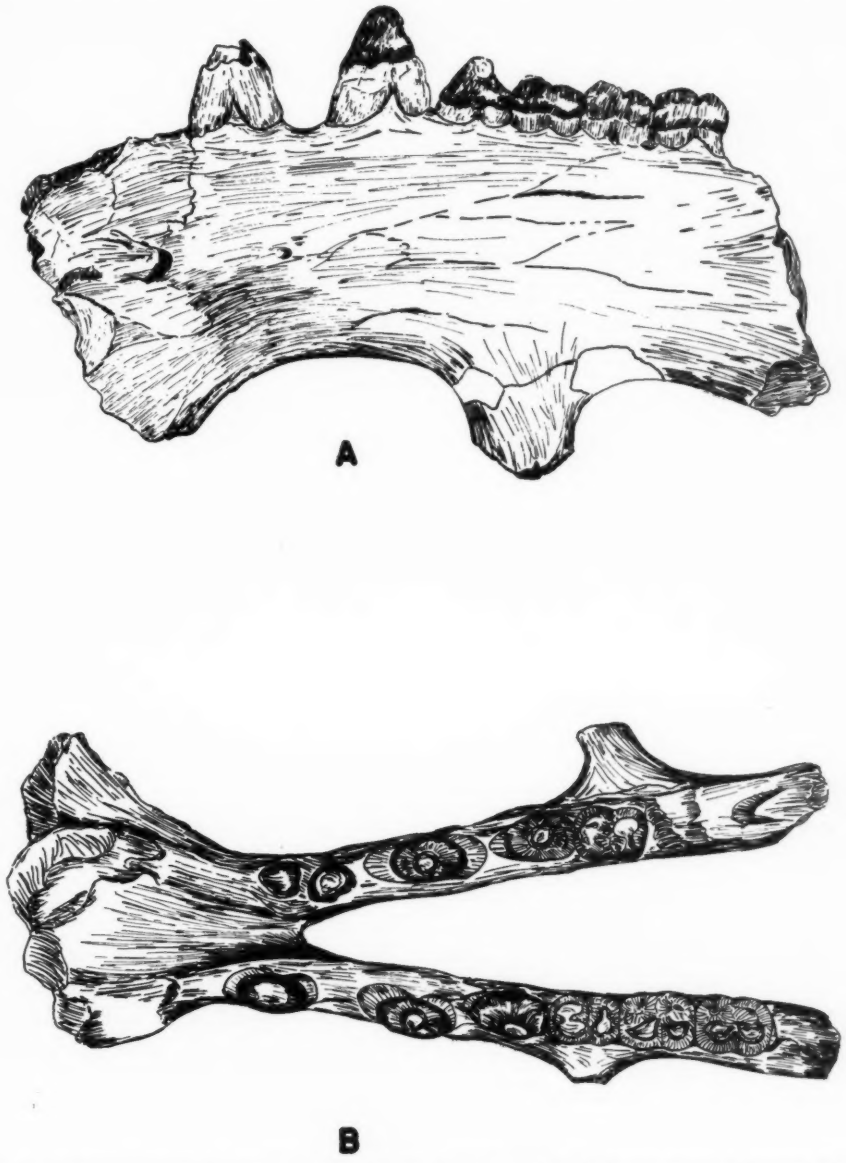

FIG. 3—*Archaeotherium* (*Pelonax*) *lemleyi* n. sp. (type specimen), lower jaws; *a*. lateral view; *b*. occlusal view. No. 2423. ×¼.

Peterson (1906) referred *Ammonodon potens* Marsh (1893) to *Pelonax* on the basis of the mental tubercle. Unlike *P. ramosus* Cope, Marsh's species has a double rooted P_2, the mental tubercle does not extend as far anteriorly as it does in Cope's species and the posterior tubercle is somewhat longer and directed anteriorly to a greater extent.

As Cope's type is edentulous we can make no direct comparisons between the sub-genotypic species and *A.* (*P.*) *lemleyi*. From the evidence offered by the alveoli we find that in *A. lemleyi* P_1 is more rounded

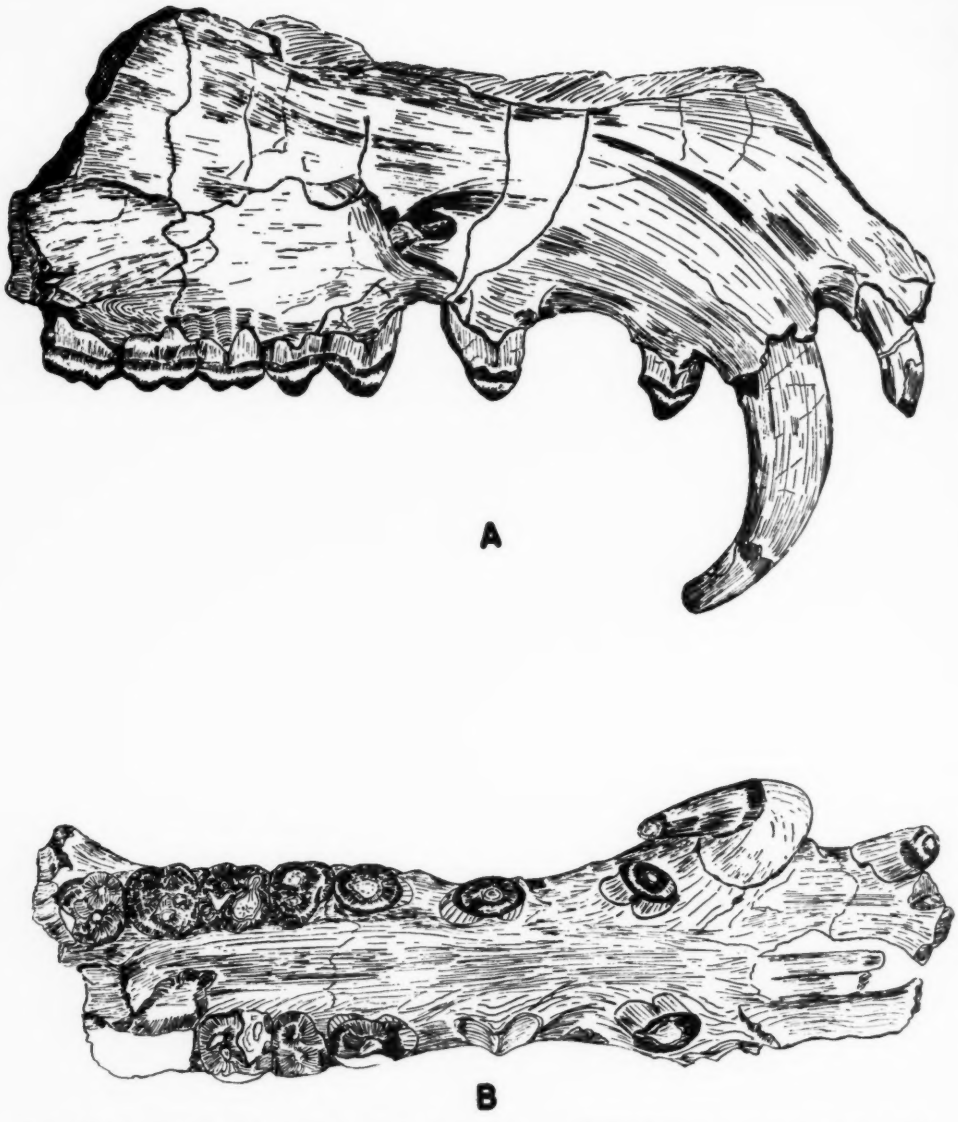

FIG. 4—*Archaeotherium* (*Pelonax*) *lemleyi* n. sp. Referred rostrum from type locality; *a*. lateral view; *b*. occlusal view. No. 4366. ×¼.

in plan; P_{1-3} are separated by long diastemas and P_1 and P_2 are double rooted. The mental process does not project forward as obliquely, and the posterior process is more slender and elongated.

A closer comparison may be made with the type of *A*. (*P*.) *potens* (Marsh) from Colorado as the molars and last premolar of this form are known. The South Dakota mandible is deeper and more massive; the anterior process heavier with a greater anteroposterior diameter; the posterior tubercle is longer and is situated below M_1 rather than below P_4. P_2 is much larger as shown by comparative measurements of the alveoli; the diastema between P_2 and P_3

is longer but the P_3's were approximately the same size by the same token. P_4 is smaller and deeply basined posteriorly in contrast to the condition in Marsh's species. The molars are similar in anteroposterior diameter, greater in transverse diameter and more closely appressed in the South Dakota species with the result that the posterior faces of the first two molars are concave. M_3 is more rectangular in plan.

The paucity of remains, three species, based on three specimens referable to the subgenus *Pelonax* makes any attempt to indicate evolutionary trends unreliable. As with so many other groups, this is another case where we must await further discoveries or the publication of information on specimens already collected.

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NEW FOSSIL FOOTPRINTS FROM THE NAVAJO(?) SANDSTONE OF COLORADO*

HENRY FAUL AND WAYNE A. ROBERTS
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ABSTRACT—The first collection of new fossil footprints from a sandstone of possible Lower Jurassic age is described. The numerous tracks and markings were made by reptiles or other vertebrates with quadrupedal and bipedal gaits, and by arachnids, a gastropod, and scolithoid and other types of "worms." The rock is purely quartzose, fine-grained, cross-bedded aeolian sandstone. The locality is about 10 miles south of Meeker, Colorado.

INTRODUCTION

Few significant fossil remains have been found in the great aeolian sandstones of the American west. Numerous footprints from the Coconino sandstone (Permian) of the Grand Canyon were first described by Lull (1918) and later extensively studied by Gilmore (1926, 1927, 1928) and Brady (1947). A small incomplete reptile skeleton was found in the Navajo sandstone and described by Camp (1936) and a fragmentary ?anchisaurid was described by Brady (1935) from the same formation. Dinosaur tracks have been observed in the Entrada (McKnight, 1941; p. 94), the Navajo (Baker, Dane and Reeside, 1936; p. 6, and Baker, 1946; p. 67), and in the Wingate (Longwell et al. 1923; p. 13), but none have been thought worthy of formal description. Baker collected a few well preserved fossil trackways in the Jurassic(?) Nugget sandstone near Lake Creek about 4 miles east of Heber, Utah; this undescribed material has been deposited in the U. S. National Museum. The tracks described in this paper bear a resemblance to some of Baker's Nugget specimens. On the other hand, the present tracks are similar to those described by Gilmore from the Coconino.

The fossil footprints were first noticed by Faul in October 1943. The single specimen collected at that time was lost, but casts made from it (fig. 6, pl. 41) at the American Museum of Natural History in New York are preserved there, and at the U. S. National Museum where the rest of the collection has been placed. The material on which this study is based was collected in the summer of 1948.

ACKNOWLEDGEMENTS

We are indebted to the U. S. National Museum, particularly to Messrs. D. H. Dunkle and C. L. Gazin, and to Professor R. S. Lull at the Yale Peabody Museum for their kind assistance in this work. We wish to thank Messrs. L. F. Brady and G. E. Lewis and Professors F. E. Peabody, R. R. Shrock and W. L. Stokes for their critical review of this manuscript, and their valuable suggestions.

We thank Mr. H. I. Sutton for his cordial coöperation in the field work.

LOCALITY

The specimens were found in the general region of Flag Creek, which flows in the valley between the Grand Hogback and Flag Ridge, south of Meeker, Rio Blanco County, Colorado. In good weather the localities are accessible by a dirt road, which extends south from Meeker by the Sutton Ranch and Rio Blanco Coal Mine to Rio Blanco. The localities are within a mile of one another, about 10 miles from

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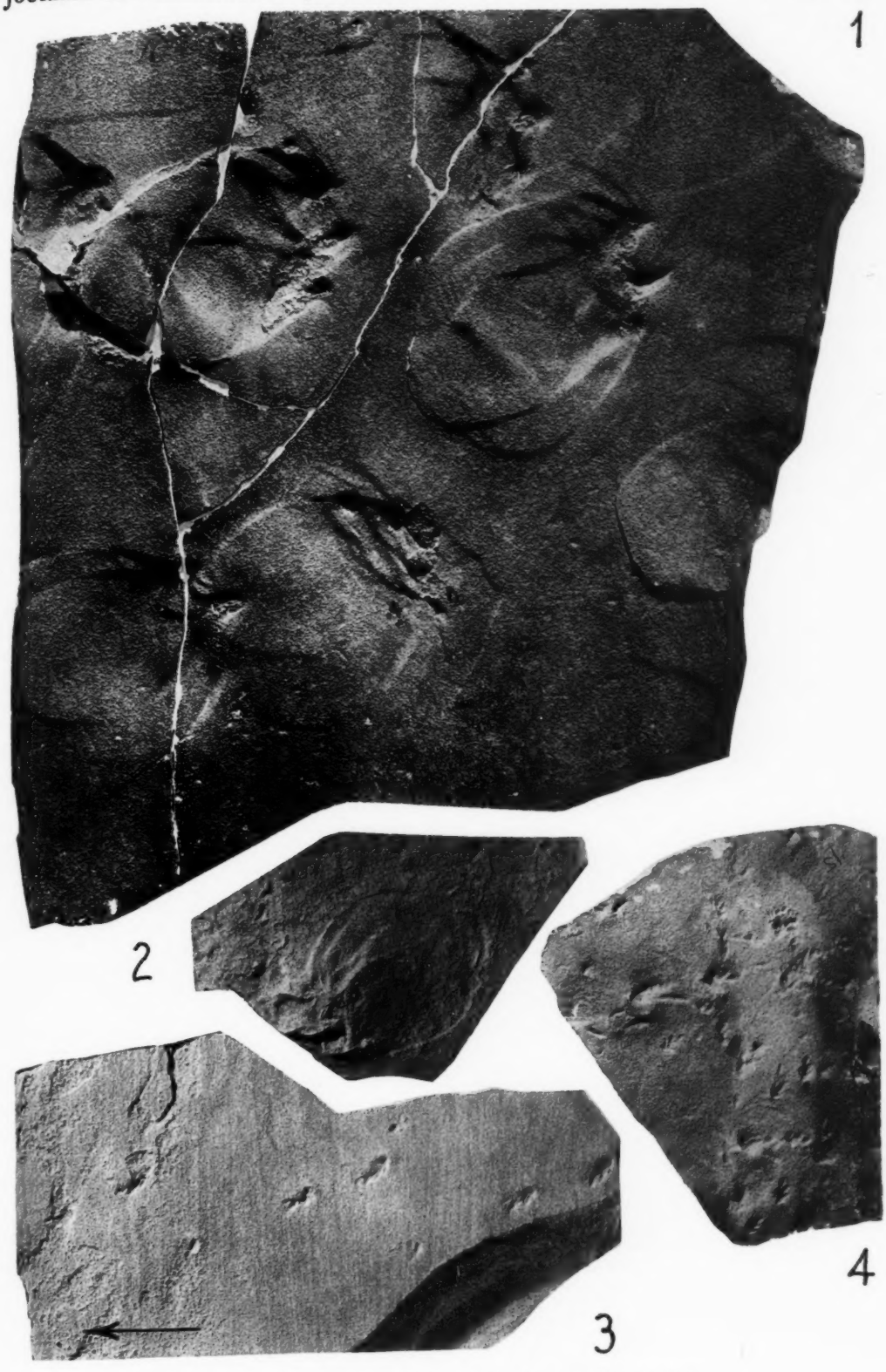
EXPLANATION OF PLATE 40

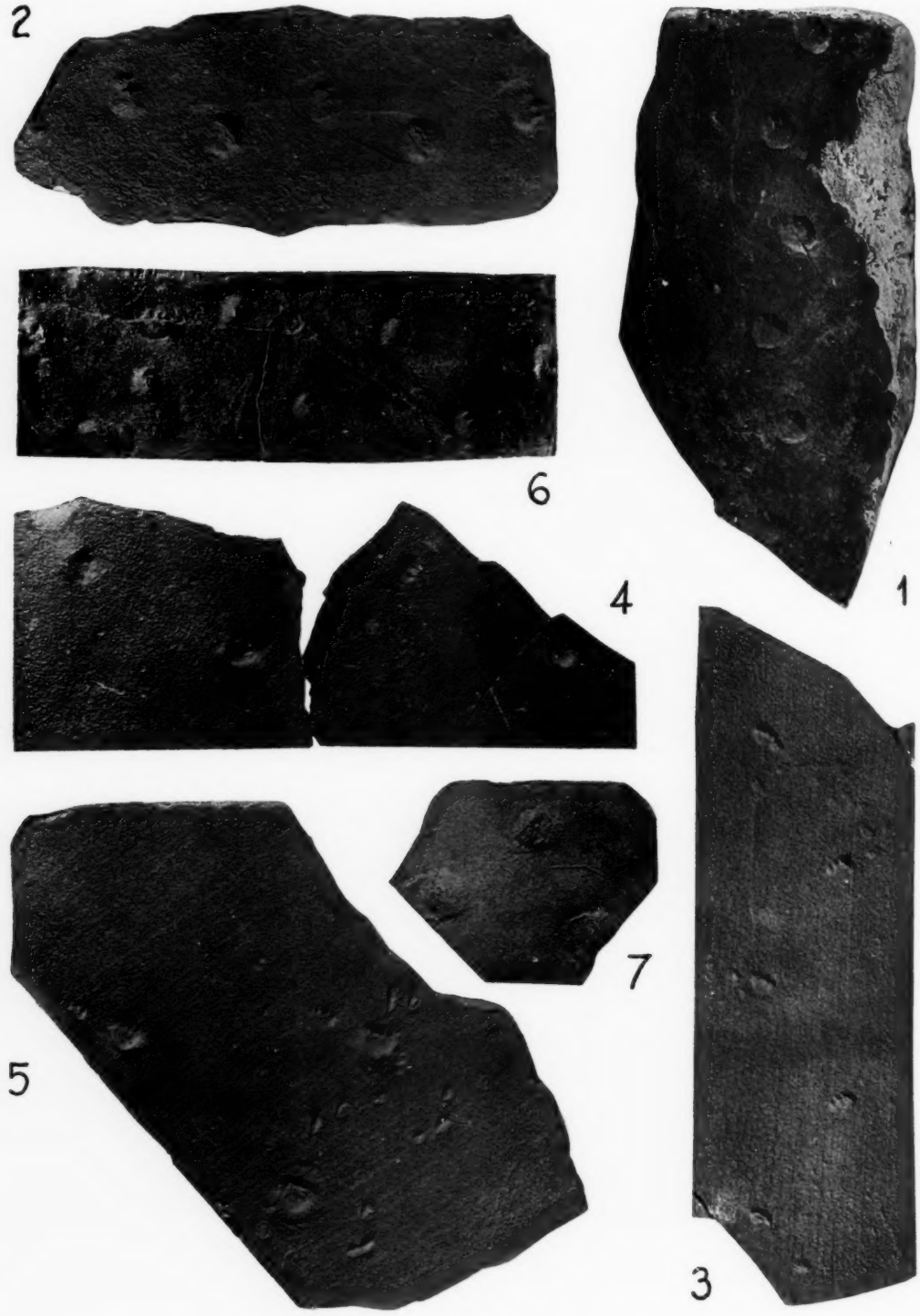
All figures are $\times\frac{1}{4}$.

FIGS. *1–2*—B 4.43, Faul and Roberts, *1*, holotype (USNM 18409); *2*, paratype, natural cast of single pes impression (USNM 18401 reverse). (p. 269)

3–4—C 4.45, Faul and Roberts, *1*, holotype (USNM 18402) painted white; *2*, paratypes (USNM 18412 A and B). (p. 270)



Faul and Roberts, Navajo? sandstone footprints



Faul and Roberts, Navajo? sandstone footprints

Meeker and 12 miles from Rio Blanco.

Most of the track-bearing slabs mentioned in this paper were quarried on the very crest of Flag Ridge (Grand Hogback quadrangle, lat. 39° 52′ 45″ N., long. 107° 54′ 20″ W.) 2½ miles S. 24° E. (true) of the Sutton Ranch. The little quarry is best reached from the road by walking up the great talus slope that covers the west flank of Flag Ridge.

Other slabs were collected on the talus slope, and still others were found loose along the ridge. One important specimen was dug up in situ about a mile north of the quarry.

Stratigraphy.—The fossils described in this paper were found in the resistant flaggy sandstone that underlies the Entrada sandstone and forms the backbone of Flag Ridge. Some geologists have included it in the Entrada (Fischer, Stokes and Smith, 1944) and given its age as Upper Jurassic. Others have referred it to the Navajo sandstone of Jurassic(?) (upper Glen Canyon) age (Baker, Dane and Reeside, 1936). We shall use the name Navajo(?) sandstone for the purpose of this paper, with the understanding that it carries no implication of prejudged age.

Lithology.—The sandstone is hard, fairly resistant, medium- to fine-grained, usually light-brown to buff in color, with long sweeping foresets that tend to dip southward. Farther south it contains the great vanadium orebody at Rifle, and it is usually massive in that region. On Flag Ridge the cement is dominantly calcareous, and the formation weathers into large flags. The weathering makes an unusually large number of bedding planes accessible to investigation and originally led us to search the slabs methodically for evidence of life, in an effort to shed some light on the admittedly uncertain stratigraphic position of the formation.

Environment.—The purity of the sandstone matrix, the frosted surface of its grains, and the aeolian type of cross-bedding all seem to indicate that wind was the depositing agent. We have confirmed Stokes' earlier observation (personal communication, 1948) that the cross beds have a tendency to dip southward, indicating that the sand came from the north. He believes that the sand may have been derived from an advancing delta, "deposited by water but not continually covered by it" (private communication, 1949).

Most of the footprints were made in dry sand (McKee, 1947), but their nature tends to support Stokes' contention of a moist climate. It is conceivable that some of the reptiles and arachnids could have ranged far and wide from any body of water, but gastropods and scolithoid "worms" were hardly equipped to survive under such conditions. We have found many pits that could be interpreted as raindrop impressions. The *B 4.43* (see Faul, elsewhere in this same issue, for explanation of nomenclature) footprints may have been made in moist sand.

The fauna.—A wide variety of animals left their footprints in the Navajo(?) sand. There are several vertebrates—almost certainly reptiles—the largest of which may have been about 3 feet long, quadrupedal with long claws, fairly heavy and probably broad in body (fig. 1). We have found only one short trackway and a solitary print of the pes of this interesting animal.

The only other quadrupedal trackway yet discovered was made by a slender lacertoid animal (*C 4.45*) with relatively long legs, and all toes but the divergent fifth turned strongly inward (fig. 2). We have

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EXPLANATION OF PLATE 41

All figures are ×½; slabs shown in figures *2*, *3* and *5* are painted white.

FIGS. *1*, *2*—E 2.4, Faul and Roberts, *1*, holotype (USNM 18404); *2*, tentatively referred specimen (USNM 18405). (p. 271)

3–7—D 4.45, Faul and Roberts, *3*, holotype (USNM 18413 B); *4*, paratype (USNM 18410) *5*, paratype (USNM 18414 A), trackway obliquely up a steep hill with heavy pes and lighter manus impressions on the right side but only very faint pes impression on the left. Two footprints of another D 4.45 and a trackway of G 8.1 are on the same slab. *6*, rubber cast of original discovery specimen, American Museum of Nat. History; *7*, tentatively referred specimen (natural cast, USNM 18406) with faint traces of tail marks. (p. 271)

several good trackways made by both large and small individuals of this species indicating possible body lengths ranging from about 6 to 12 inches in different individuals. Most of the trackways are well impressed on one side but have only light digital impressions on the other, and usually run along the contour of the sloping sand. One would conclude that this creature walked with the body held high off the ground. Most trackways show a regular pace; one or two slabs are covered with a jumbled profusion of imprints.

The two remaining small vertebrates of this fauna seemingly preferred the bipedal mode of locomotion. *D 4.45* (fig. 3) was the larger of the two, a small, gaunt, long-legged creature, hardly more than a foot high. He walked erect, striding the sand with a broad, regular pace, his small round four-toed (?) foot turned inward. On steep slopes the downhill manus is impressed occasionally. The other comparatively rare biped (*E 2.4:* see fig. 4) was of similar stature, if not a bit larger. He was perhaps heavier than the animal of *D 4.45*. The foot was round, toes directed forward, and the trackways straight and narrow.

The bipedal gait of *D 4.45* and *E 2.4* may be only apparent, and "due largely to the fact that most of the weight was on the pes, except when the animal was moving very slowly. When running, all the weight may be aft." (Brady, private communication.)

It is interesting that only one of the trackways we have found shows a tail drag. The slab (USNM 18406) shows three very indistinct footprints with a faint tail mark between them. The animals seem to have been able to walk quite well on two feet without touching the ground with their tails.

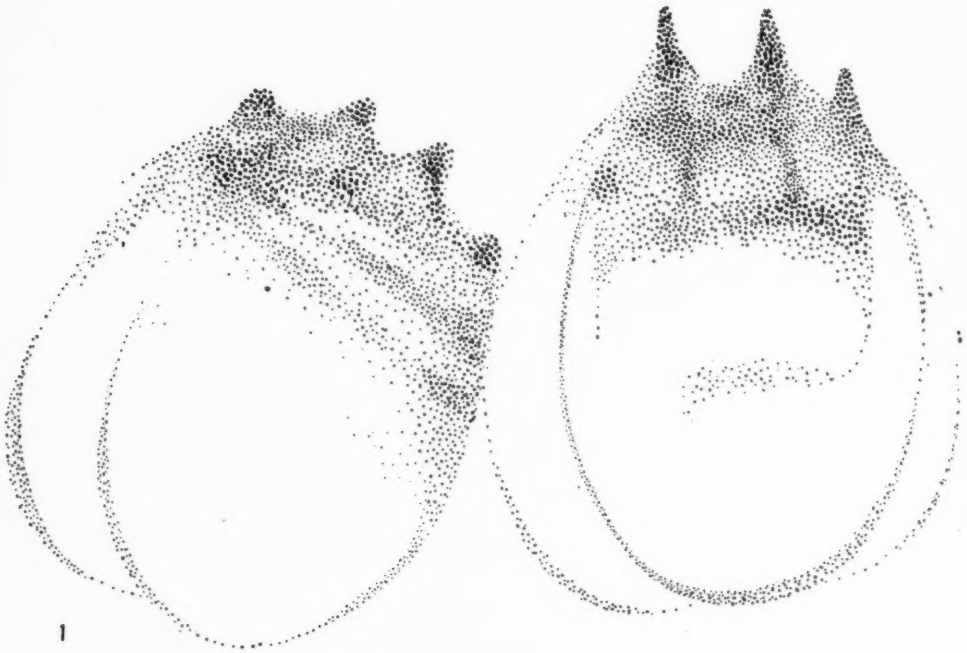


FIG. *1*—Footprints of the largest quadruped, probably a reptile, ×½.

Actually the best trackways collected on Flag Ridge were made by eight-footed creatures (presumably arachnids). The *G 8.1* trackway shown on figure 3 of plate 42 answers the generic description of *Octopodichnus* Gilmore, probably the track of a scorpion or a large spider. We have found two other slabs (figures 1 and 2 of pl. 42) with clear, long, invertebrate trackways. We described them as *F 8.1*, and we are of the opinion that the trackways were made

by large scorpions, in view of their striking similarity to the trackways of recent scorpions on dry sand (Brady, 1947, fig. 2 of pl. 66). None of our trackways, however, shows any trace of the tail drag that is frequently found in scorpion trackways.

A shallow, irregularly sinuous and annulate trail was found on one of the slabs, (fig. 3 of pl. 43) in association with a vertebrate (*D 4.45*) trackway. Similar marks have been ascribed to gastropods by the Fentons (1931), and Abel (1935, p. 207 et seq., figs. 176–195) has shown photographs of trails made by a recent, blind, burrowing species (*Bullia rhodostoma* Gray) on a South African beach. Our trail shows striking similarity to those made by *Bullia* and there seems little doubt in interpreting it as the mark of a gastropod.

Three types of "worm burrows" also have been collected. One of the specimens shows burrows of a scolithoid type (fig. 1 of pl. 43), another slab is covered with irregular trails or castings, some with short branches (fig. 4 of pl. 43), whereas the third shows a single non-annulate, sharply sinuous trail, preserved as a cast on the lower surface of a slab (fig. 2 of pl. 43). The specimens hardly warrant description.

FIGS. *2–4*—Trackways, ×1. *2*, C 4.45. *3*, D 4.45. *4*, E 2.4.

SYSTEMATIC DESCRIPTION

VERTEBRATES (REPTILIA?)

B 4.43

Characters.—Quadrupedal gait, plantigrade, manus and pes oval, subequal in size, with three heavy claws on pes impression and four (?) smaller ones on manus. Digits probably very short with respect to

length of sole, and all of subequal length, pointing forward or slightly inward. Heel well rounded.

Holotype.—USNM 18409, trackway of 3 or 4 consecutive paces (fig. 1 of pl. 40).

Paratype.—USNM 18401 (reversed side), cast of single pes impression.

Locality.—Found in situ, 2½ miles S. 24° E. of Sutton Ranch.

Measurements.—Stride unknown, track width 35 cm. (estimated), pace angulation unknown, maximum length of pes 15.5 cm. (holotype) and 13.5 cm. (paratype), manus approximately 14 cm.; width of manus and pes approximately 10 cm.

Description and Discussion. B 4.43 was made by a creature at least three times larger and certainly very much heavier than the animals that left the other trackways.

The footprint indicates a flat-soled oval pes and manus. The median claw of the pes is somewhat longer and sharper than the others, but the claws of the manus are approximately equal in length. Digits are not separately discernible in the footprint, except for the impression of the claws. We believe that USNM 18409 is a trackway impressed in damp sand. Much of the footprint is actually displaced sand, and the measured size of the footprint probably exceeds dimensions of the foot.

The trackway is too short to permit estimates of length of stride, although one might infer that it was about as long as the track is wide, about 30–40 cm. or perhaps longer. These tracks were made probably by an animal just getting underway from a standing position.

C 4.45

Characters.—Quadrupedal gait, semiplantigrade, manus and pes lacertoid, subtriangular, strongly asymmetrical. Manus print placed well ahead of pes print and inward. Pes larger than manus, with five digits, increasing in length from I to V. Digits I–IV turned strongly inward, digit V divergent, pointing straight forward, its apparent length probably exaggerated by forward drag of pes after impression. Manus impression shows only four digits, length increasing I–III, IV slightly shorter than III, all pointed inward. All digits straight, distally tapering, not visibly articulated, about ⅓ as long as entire footprint, on the average.

Holotype.—USNM 18402, trackway of 5 consecutive paces (fig. 3 of pl. 40)

Paratypes.—USNM 18412A, trackway of 7 probably consecutive paces; USNM 18412B, imprint of pes and manus.

Referred Specimens.—USNM 18401A and B, two fragmentary trackways and many isolated prints of pes and manus.

Locality.—Type was found in situ 1½ miles S. 51° E. of Sutton Ranch, paratypes were quarried 2½ miles S. 24° E. of the ranch.

Measurements.—Stride 13.8 cm. (type), 7.5 cm. (paratype A), approximately 14 cm. (paratype B); track width approximately 8 cm. (type); pace angulation 80°; max. length of pes approximately 2.8 cm., manus approximately 2.3 cm.; width of pes and manus slightly less than roughly ½ their length, but exact width unknown.

Discussion.—C 4.45 almost certainly was a lizard. The footprints are long and slender with the apparently clawless digits clearly impressed. Digits I–IV probably carried much of the weight of the animal, but the heel also is impressed, expecially on prints of the pes. There is no trace of a tail drag.

Disparity in size of individuals is pronounced, reaching a factor of more than two between some.

Pes.—Length of pes varies from about 17 mm. to more than 30 mm. for different individuals. Assuming a pes length of 30 mm., the digit lengths would be approximately: I—4 mm., II—7 mm., III—8 mm., IV—9 mm., V—perhaps 13 mm. The heel is narrow but well rounded. The prints are not clear enough to show details of the plantar surface.

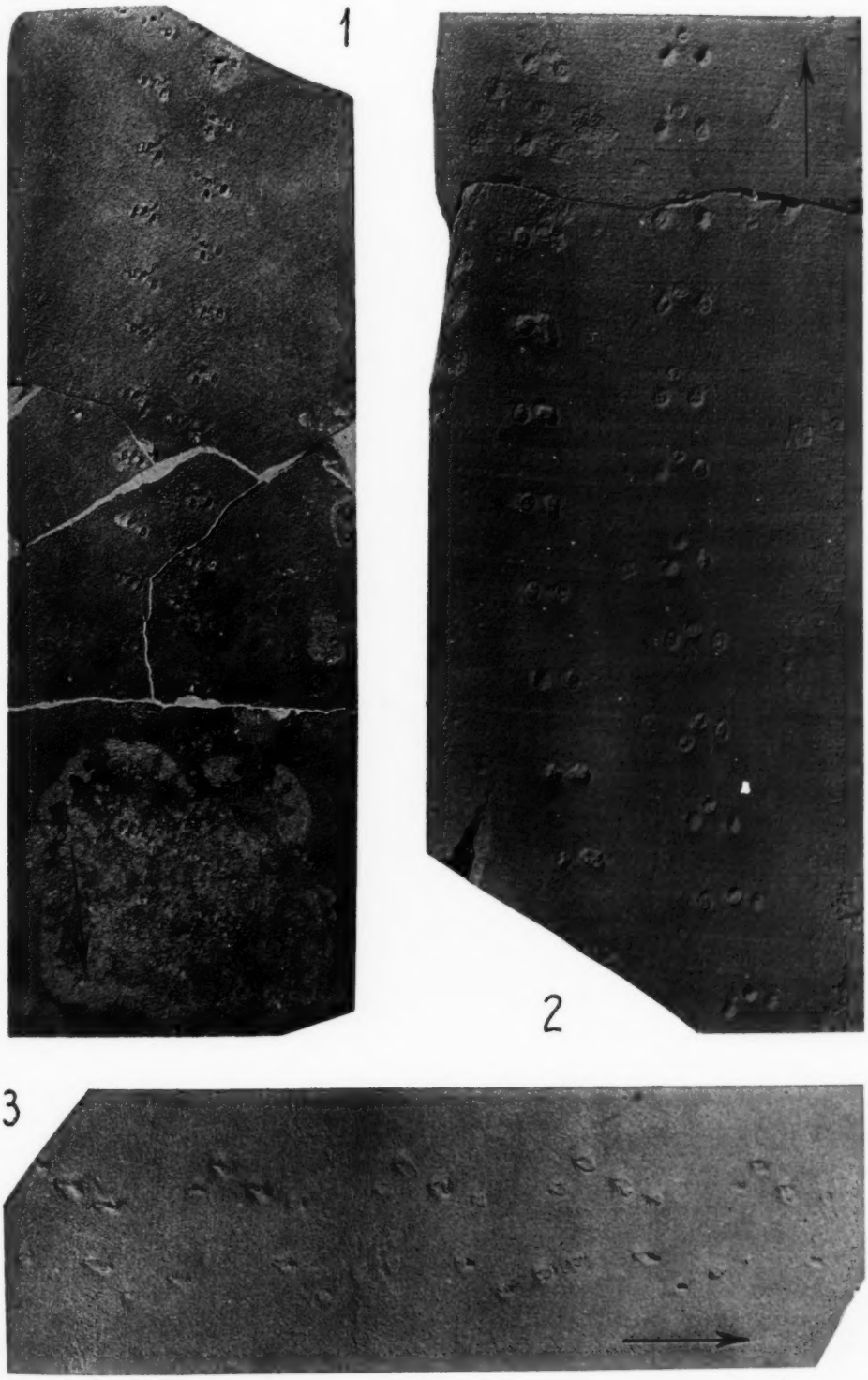
Manus.—With a manus about 22 mm.

EXPLANATION OF PLATE 42

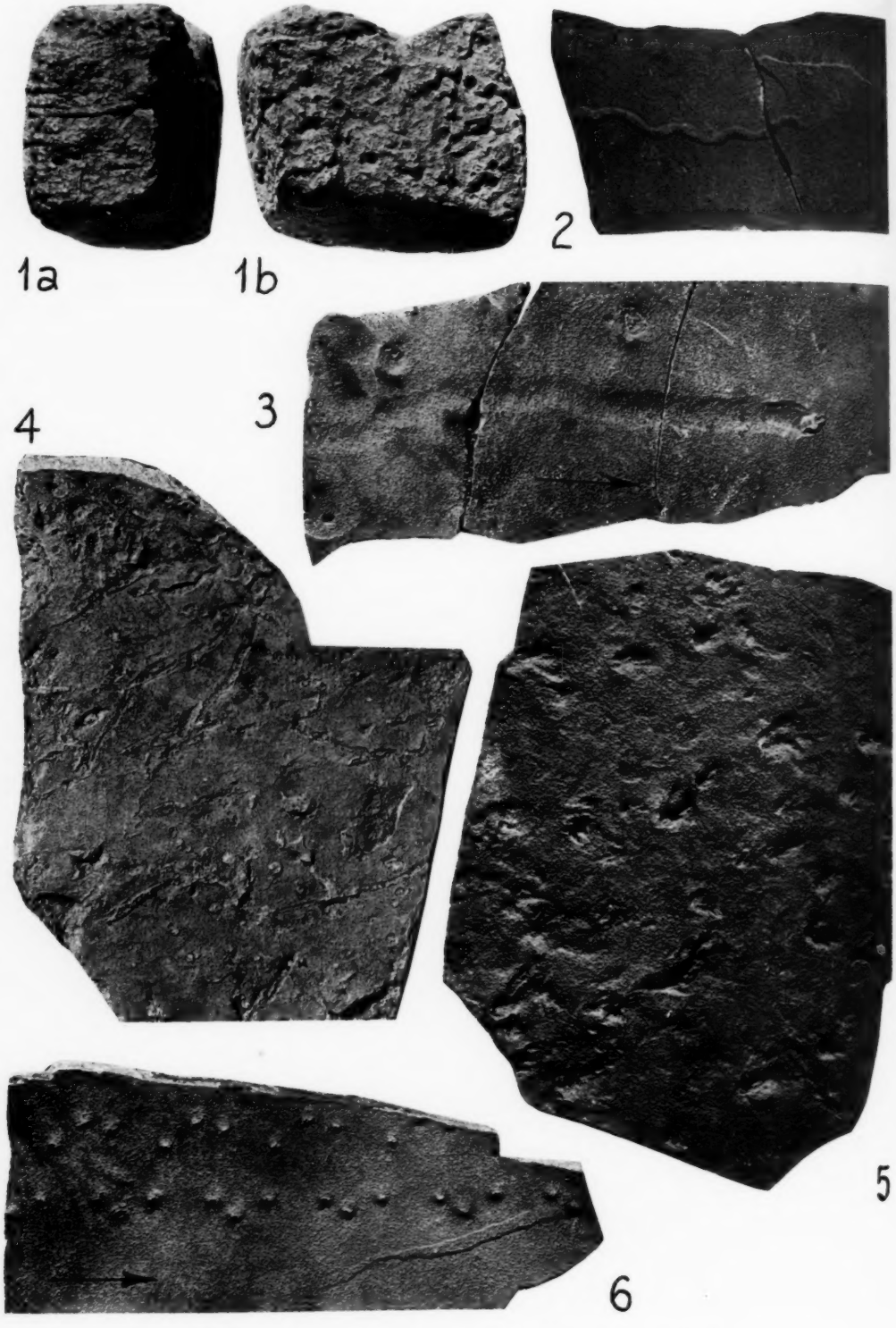
All figures are ×¼. Arrows indicate direction of motion. Figures *2* and *3* are painted white.

FIGS. *1*, *2*—F 8.1, Faul and Roberts, *1*, holotype (USNM 18411); *2*, unusually large specimen of arachnoid trackway (USNM 18407), tentatively referred to F 8.1. (p. 272)

3—G 8.1, Faul and Roberts, holotype (USNM 18415). (p. 274)



Faul and Roberts, Navajo? sandstone footprints



Faul and Roberts, Navajo? sandstone footprints

long, the digits would measure approximately: I—3 mm., II—5 mm., III—7 mm., IV—6 mm. The trackway made by the manus is only about half as wide as the trackway made by the pes.

D 4.45

Generic Characteristics.—Semi-bipedal gait, manus rarely touching the ground. Semi-digitigrade, subround pes probably pentadactyl, but only three or four digits usually impressed. Manus digitigrade, smaller than pes, possibly tetradactyl, placed behind pes and inward. Digits of manus and pes very short, stubby, apparently clawless, probably subequal in size, symmetrically increasing toward center. All digits turned strongly inward. Pes impression wider than long. The trackway is unusually broad for a biped.

D 4.45 is similar to *Palaeopus* Gilmore (1926). It differs from it in the relative position of the manus, and the inward turn of digits.

Holotype.—USNM 18413 B, trackway of five consecutive paces (pl. 41, fig. 3).

Paratypes.—USNM 18410, trackway of four consecutive paces, and USNM 18414A, trackway of three consecutive paces.

Referred Specimens.—USNM 18416A, USNM 18403 and plaster cast in American Museum Nat. Hist. (fig. 6 of pl. 41).

Locality.—Type and paratypes found in situ, 2½ miles S. 24° E. of Sutton Ranch.

Measurements.—Stride: Type: 13.5 cm., Paratypes: 18 cm. and 14.4 cm., other specimens have strides of 9 cm., 9.6 cm. and 14 cm. Track width: 5.7–6.5 cm.; pace angulation: 110°; length of pes imprint 1.2 cm., manus length unknown. Width of pes 1.7 cm., inferred width of manus about ⅓ less.

Discussion.—*D 4.45* apparently was made by a slender animal with long and powerful hind legs and small forelegs. The center of gravity was fairly high in the body, and the creature normally used the bipedal gait. We have found only two impressions of the manus, made where the animal was walking obliquely up a steep slope and the going must have been a little tough.

D 4.45 is the most common footprint in the Navajo(?) fauna. The trackways are straight and regular, resembling *Paleopus regularis* Gilmore in that way. The stride is long compared to the size of the foot, and varied with the speed of the walking animal. The track width is almost constant, and all footprints are roughly equal in size.

Pes.—The footprints are short and broad with most of the weight carried by digits II–IV, which are the most clearly impressed. No claw marks are apparent. The digits turn strongly inward but the footprints are roughly symmetrical about the axis of the pes. The digits appear to have the length of only a few mm. before fusing into the sole.

Manus.—The manus is not well known from the material available at present. It is clawless and smaller than the pes. One of the manus impressions shows three and the other four (?) digits.

A small slab bearing a trackway of three obscure bipedal steps tentatively referred to this "species," shows a faint but clear continuous sinusoidal tail mark between the footprints. The inferred tail was comparatively short, pointed, and probably touched the ground about half a stride (one pace) behind the pedes.

E 2.4

Characters.—Bipedal gait, semi-plantigrade. Pes impression round, symmetrical with four short subequal digits, probably with small claws. Digits short, sharply tapered distally, point directly forward, and may have pronounced plantar pads. Trackway very narrow, less than ⅓ of the length of stride. Ratio of print length to length of stride is about 1:6.

EXPLANATION OF PLATE 43

All figures are ×¼. Arrows indicate direction of motion (where known).

FIG. *1*—Scolithoid burrows; *a*, side view; *b*, plan view. (USNM 18421). (p. 267)

2—Natural cast of sinuous invertebrate trail (USNM 18416, reverse).

3—Gastropod trail associated with D 4.45 trackway (USNM 18416). (p. 269)

4—Slab with supposed invertebrate burrows and castings (USNM 18422).

5—Slab with many fragmentary trackways of C 4.45 etc. (USNM 18401). (p. 270)

6—G 8.1, Faul and Roberts (natural cast) paratype, with impressions of fourth feet missing (USNM 18417). (p. 274)

Holotype.—USNM 18404, trackway of six consecutive paces (fig. 1 of pl. 41).

Referred Specimen.—USNM 18405, a trackway of five consecutive paces, is tentatively referred to this species.

Locality.—The holotype was found in the float on the talus slope below the quarry and the referred specimen was collected loose on Flag Ridge, some 300 yards south of the quarry.

Measurements.—Stride 11.1 cm.; track width 3.3 cm.; pace angulation: 150°; maximum length of pes 1.8 cm., width of pes 1.9 cm.; manus unknown.

Discussion.—Judging by the very narrow bipedal tread, *E 2.4* was made by a slender, long-legged animal that walked erect with almost human posture. The gait is regular and footprints well impressed.

The broad outline of the footprint is circular, but it is not altogether clear how the weight was divided between sole and digits. The digits probably carried small, sharp claws. Digits were subequal in length, increasing toward the center. No more than four digits can be counted in any footprint, and their length is difficult to determine. They were probably short and stubby, possibly with a bulbous pad on the distal end.

Characteristic features are the narrow trackway and round footprints.

Invertebrates

F 8.1

Generic Characters.—Track of eight-footed animal. Irregular clusters of two, three, or four simple, small, round foot impressions alternating along medial line. Trackway broader than length of stride.

The similarity between *F 8.1* and *Paleohelcura* (Gilmore, 1926, emended by Brady, 1947) is not immediately obvious. *Paleohelcura* is described as follows: "Foot apparently tridactylous; long axis of each cluster of three placed strongly diagonal (divergent) to direction of movement. Tail trace sometimes present." In his experiments with live scorpions, however, Brady has demonstrated that the recent scorpion *Centruroides sculpturatus* makes a track very similar to *Paleohelcura tridactyla* Gilmore at a temperature of 15°C. and on dry sand. He concludes that "*Paleohelcura* should be tentatively referred to a member of the Scorpionida." At 8°C., the same scorpion impresses all eight feet and leaves a trackway similar to *F 8.1*, though much smaller. Therefore it seems likely that *F 8.1* also was made by a scorpion.

Holotype.—USNM 18411, trackway of 33 consecutive paces (fig. 1 of pl. 42).

Referred Specimens.—USNM 18415B, an indistinct trackway of about 15 consecutive paces.

Locality.—Talus slope below the quarry, about 2¼ miles SSE from Sutton Ranch.

Measurements.—Stride: 3.4 cm.; track width: 5.1 cm. All footprints of a cluster usually fall within a circle 1.6 cm. in diameter. Pace angulation: approximately 50°, measured center to center of footprint groups.

Discussion.—*F 8.1* was made by the smallest of the presumably arachnoid animals of the Navajo(?) fauna. If it was indeed a scorpion, it could have been about 4 inches long.

The long trackways are seldom straight but generally curve broadly. In contrast, "the straightness of the Coconino trackways is remarkable." (Brady, private communication.) There are usually four simple round footprints in each cluster, but one or two feet sometimes fail to impress. We have never observed any tail marks.

One slab found in the float near the quarry (USNM 18407) bears an unusually large arachnoid trackway with a stride of 5.2 cm., a track width of 10.5 cm., and pace angulation of approximately 34° (fig. 2 of pl. 42). Footprints of each cluster fall within a circle 3 cm. in diameter and there are only two or three footprints per cluster. The step is somewhat shorter than in the smaller specimens. We tentatively refer this specimen to *F 8.1*. The creature that made the track may have been about 8 inches long.

Genus Octopodichnus Gilmore (1927), emend. Brady (1947)

Generic Characters: The track of an eight-footed animal, with individual impressions arranged in alternating groups of four. Any of the individual footprints may be simple elongated impressions or may be apparently prints of a didactyle or even tridactyle extremity.

Neither Gilmore nor Brady make any mention of the characteristic regularity of the footprint clusters which distinguishes *Octopodichnus* from the other eight-footed trackways. It may be well to emend the

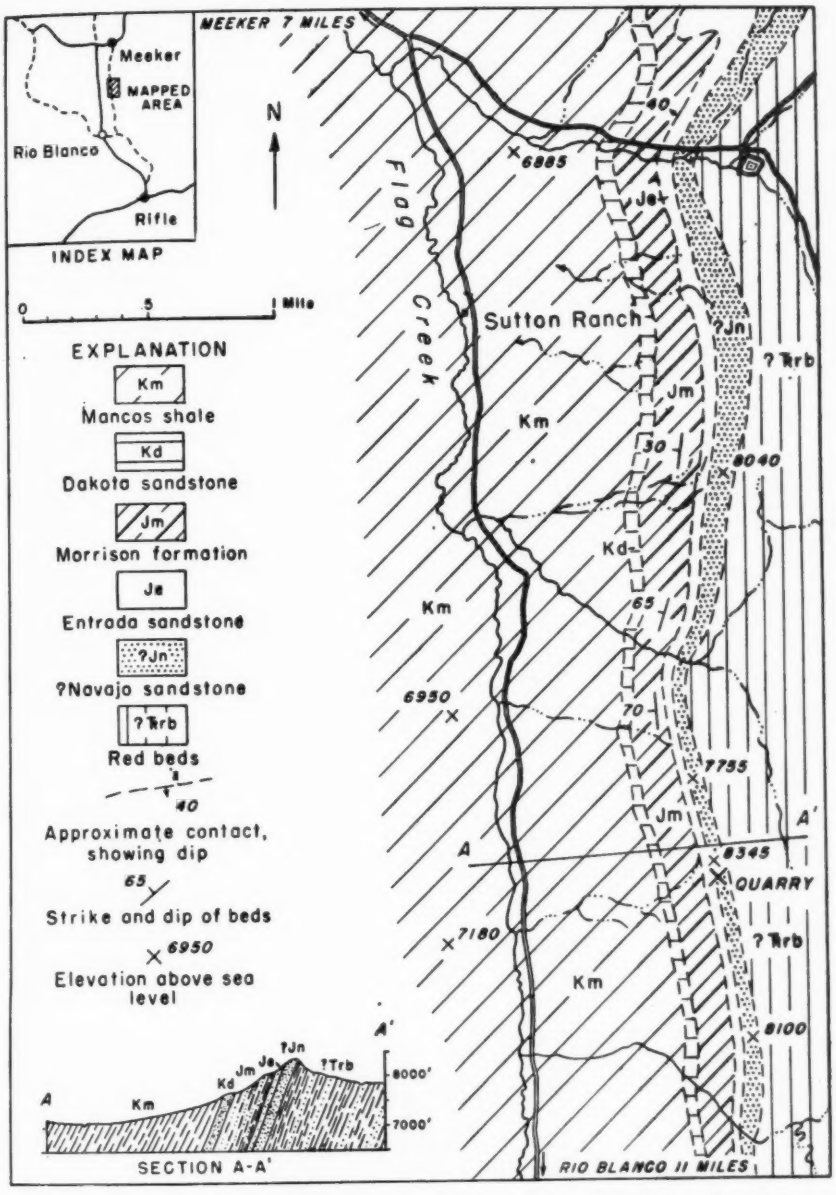


FIG. 5—Geologic map of the Sutton Ranch area, Colorado, showing the location of the quarry which furnished most of the tracks.

generic definition further to include the statement: Imprints form regular pattern. 1-2-3 fall on line oblique to line of movement with 4 inward and back of 3.

The nature of *Octopodichnus* remains uncertain. Gilmore (1928) concluded "that the trackway was probably made by a Permian crustacean" perhaps similar to the recent sand crab *Ocypoda albicans*. Abel (1935) spent some time in the Grand Canyon, examined Gilmore's material, and collaborated with W. Kühnelt in some experiments with spiders at the Zoological Institute of the University of Vienna. He concludes that the track was made by a large solifugoid spider. Such spiders are known to possess

two large claws on their extremities. Some species are swift animals of prey and attack lizards and other small creatures. Brady (1947) suggests, on the other hand, that "*Octopodichnus* may very possibly be the track of a large scorpionid with well-developed and movable basal spines." Further experiments may help to settle the differences of opinion.

G 8.1

Holotype.—USNM 18415A, trackway of 11 consecutive paces (fig. 3 of pl. 42).

Paratype.—USNM 18417 trackway of nine consecutive paces.

Referred Specimen.—USNM 18414B, trackway of five consecutive paces.

Locality.—USNM 18415 was found in the float, 50 feet below the quarry; USNM 18414 and USNM 18417 were quarried 2½ miles S. 24° E. of Sutton Ranch.

Measurements.—Stride: USNM 18415: 11.1 cm., USNM 18417: 6.6 cm.; USNM 18414B: 8.2 cm. Track widths: 8.5 cm., 5.9 cm., and 6.5 cm. respectively. Distance (holotype) imprints 1–3: approximately 4.5 cm., imprints 3–4: approximately 2.2 cm. Angle 1-3-4 aproximately 120°.

Discussion.—Compared to trackways of recent arachnids, *G 8.1* is rather large. If the track was made by a crab, however, its size is less impressive, compared to some of the very large Polynesian species. It is our opinion that the crab hypothesis seems less probable than the other two, in view of the clear frontal manner of locomotion.

From the material collected so far, it is difficult to decide if any of the appendages of *G 8.1* possessed the claws or spines that impressed so clearly in most trackways of *O. didactylus* Gilmore. It is our opinion that these projections were small in *G 8.1*, if they existed at all. Most of the footprints appear to have been made by a simple, pointed foot on all of the four extremities. Foot 1 occasionally fails to impress. In other respects the new footprints resemble *O. didactylus* Gilmore, though the average size of the latter is somewhat greater.

O. minor is didactyle and considerably smaller, on the average, than *G 8.1*.

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FAUNA AND PALEOECOLOGY OF THE UPPER CAMBRIAN WARRIOR FORMATION OF CENTRAL PENNSYLVANIA

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ABSTRACT—The known fauna of the Upper Cambrian Warrior limestone of central Pennsylvania is expanded by systematic description of an additional 34 species and three varieties of trilobites belonging to 18 genera. Of these, one genus, 24 species, and three varieties are new. Supplementary descriptions are given of previously recognized trilobite and brachiopod species not heretofore reported from the Warrior.

Data showing facies and faunal occurrences are given for a measured section of 746 ± feet near Waddle, Pennsylvania. Trilobites collected from this section reveal a *Crepicephalus* fauna in the upper hundred feet, underlain by a *Cedaria* fauna. Compared with trilobites which Butts collected from the type locality at Warriorsmark and which are identified here, the following relationships are clearly indicated: the *Cedaria* zones at both localities contain three of the same trilobite species and are probably age equivalents; species of the new genus *Llanoaspidella* occur at both localities. Other relationships are less clear and the apparently anomalous occurrence of certain key genera of the *Crepicephalus* and *Cedaria* zones give rise to certain problems which are discussed.

Faunal and lithologic relationships in late Warrior time are studied and interpreted as indicating a cycle of alternations between three different environments, namely, clear water *Cryptozoon* reefs, clay turbid water, and tidal flats.

INTRODUCTION

THE results of a paleontological study of the trilobite and brachiopod fauna discovered in the Warrior limestone formation of central Pennsylvania are given in the present paper. The material for this study came from the Smithsonian Institution Warrior collection augmented by the Pennsylvania State College's and the writer's own collections. The Smithsonian material was collected by Walcott, Ulrich, Butts, and Resser in the period from 1910 to 1920 in connection with Butts' areal and stratigraphic mapping of the Bellefonte, Tyrone, Huntingdon, and Hollidaysburg Quadrangles (Butts, 1918, 1936, 1939, 1945). The College material was collected at various times by faculty and students during field trips. The writer's material was collected during the summer of 1949 from a measured section.

During the course of this study, the author has benefited from the helpful criticism and guidance of Professor Frank M. Swartz, under whose supervision the study was presented in partial fulfillment of the requirements for a Master of Science degree at the Pennsylvania State College. To both Dr. G. Arthur Cooper, who sponsored the loan of the Smithsonian Warrior collection for the purpose of the present investigation, and in other ways demonstrated his helpful interest, and to the Director of the Smithsonian Institution, who made the loan possible, the author wishes to express his indebtedness. Several students of the Cambrian furnished the writer with helpful paleontologic information or loan of material: Dr. Cecil H. Kindle, Dr. Christina Lochman Balk, Dr. Franco Rasetti. Appreciation is extended to Dr. William Spackman for valuable criticism of the original manuscript. Laboratory and photographic facilities, as well as Warrior fossils in the school collections, were generously made available by the Pennsylvania State College School of Mineral Industries.

Tasch Collection Localities

Exposures were measured along Highway No. 322 leading to Port Matilda, about 5 miles west of State College, Pennsylvania. A more detailed section is given than usual to preserve the identity of such facies as

FOSSIL LOCALITIES

Smithsonian Collection Localities

Locality Number	
24-b	Half a mile southeast of Waddle, Pennsylvania.
24-c	Half a mile south of Waddle, Pennsylvania.
25-g	One mile south of Waddle, Pennsylvania.
24-i	One and one-quarter miles south of Waddle, Pennsylvania.
24-e	Two miles southwest of Waddle, Pennsylvania.
24-d	Two and three-quarter miles southwest of Waddle, Pennsylvania.
107-k	Two miles north of Benore, P. O. (same as locality 7341 Bellefonte Quadrangle).
62-b	Hollidaysburg Quadrangle, Pennsylvania.
24-h	Six miles south of Roaring Spring, Pennsylvania.
24-f	At elbow of road along Warrior Run, one mile southeast of Warriorsmark, Pennsylvania. Upper third of Warrior limestone.
24-g	A quarter of a mile southeast of Warriorsmark, Pennsylvania. Lower part of Warrior limestone.

The Pennsylvania State College Collection Localities

Locality Number	
——	Friend's Cove: Half a mile northeast of Hartley, Pennsylvania, in southwestern part of Everett Quadrangle.
——	Schneider Farm: 3¼ to 4 miles south of Baker Summit, Pennsylvania, in northern part of Everett Quadrangle.
	Half a mile south of Waddle crossroads, same as locality "24-c" above.

Grid coordinates on Bellefonte quadrangle:

7259	One and one-half miles southwest of Waddle, Pennsylvania.
7285	Two and one-quarter miles southwest of Waddle, Pennsylvania.
7291	One and three-quarter miles southwest of Waddle, Pennsylvania.
7294	One and seven-eighths miles southwest of Waddle, Pennsylvania.
7341	Three-fourths of a mile southwest of Waddle, Pennsylvania.
Old Quarry	Three-fourths of a mile south of Waddle, Pennsylvania.

Top of the Warrior Formation (Warrior-Gatesburg contact concealed: soil cover of Gatesburg sandstone containing some displaced Gatesburg rock. Distance of bed 13.9 to first Gatesburg exposure, a quarter of a mile). Subtotals indicated by boldface type.

		Thickness in Feet	
		Bed	Total
13.9	Covered interval. 17.5′ below top of the formation, a fossiliferous bed contained: *Blountia prolifica, Coosella convexa, Coosella*, sp. no. 2, *Coosella* aff. *convexa, Hyolithes* sp.	62.5	**107.3±**
13.8	Fine-grained limestone, edgewise conglomerate facies. Between the ninth and sixteenth inch; *Lingulepis acuminata*	2.2	44.8
13.7–13.5	Coarse-grained to oolitic limestone; dolomitic limestone; oolitic facies upper portion; edgewise conglomerate facies; thin-bedded to massive limestone	3.1	42.6
13.4	Sandy, fine- to coarse-grained limestone, lower part dolomitic; edgewise conglomerate facies. Lower portion near road level contains: *Coosella convexa, Blountia* sp. no. 1	1.6	39.5
13.3	Coarse-grained limestone, upper five inches very fossiliferous: *Coosia? pustulata, Coosella* sp. no. 2, *Blountia prolifica, Tricrepicephalus arcuatus, Coosella* aff. *convexa*	1.5	37.9
13.2	Coarse-grained limestone, above first four inches fossiliferous: *Coosia? pustulata, Crepicephalus* sp. no. 1, *Coosella convexa;* massive limestone overlies oolitic facies	1.4	36.4
13.1	Fine- to coarse-grained dolomitic limestone. (Base 0.35 mile southeast of Waddle Road)	35.0	35.0
13.0	Covered interval (included is a small exposure inset from road as ledge of hill—coarse-grained oolitic to sandy massive limestone)		**287.5±**
12.102–12.100	Massive to coarse-grained sandy limestone	2.6	**104.7±**

		Thickness in Feet	
		Bed	Total
12.99	Covered	6.9	102.1
12.98	Granular, coarse-grained, micaceous limestone	1.0	95.2
12.97	Coarse-grained limestone, fossiliferous near reef facies. Upper six inches *Cryptozoon undulatum* (with concentric rings one inch in diameter). Thickness of reef-facies in lower portion of bed, 9 inches: *Blountia prolifica, Coosia* sp., *Kingstonia apion*	3.5	94.2
12.96	Covered	1.1	90.7
12.95–12.85	Alternating beds of massive dolomitic limestone and thin-bedded limestone and shales	4.1	89.6
12.84	Fine- to coarse-grained limestone: *Kingstonia apion*	2.1	85.5
12.83	Massive limestone	2.1	83.4
12.82	Massive limestone, lower part sandy, granular limestone, fossiliferous: *Kingstonia walcotti, Kingstonia ulrichi, Kingstonia apion*	1.0	81.3
12.81	Black oolitic limestone containing *Kingstonia ulrichi, Kingstonia trapezoidea*	0.7	80.3
12.80	*Cryptozoon undulatum*	0.6	79.6
12.79	Granular sandy limestone, upper portion fossiliferous: *Kingstonia ulrichi, Kingstonia trapezoidia, Kingstonia apion, Kingstonia walcotti, Coosella convexa, Coosella* sp. no. 2. Lower portion, three-inch black oolitic facies interfingers upper part of bed	0.9	79.0
12.78	*Cryptozoon undulatum* (with concentric rings ½–1 inch in diameter); clay, pebble-like concretions, bean shaped	0.8	78.1
12.77	Massive limestone, fossiliferous directly above *Cryptozoon* reef facies; deep, sandy weathering: *Coosella convexa*	2.4	77.3
12.76	*Cryptozoon undulatum*	0.7	74.9
12.75	Coarse-grained to granular limestone; when cracked, sandy interior; 31 to 38 inches above bottom of bed 12.75 there occurs a thickness of 7 inches that is fossiliferous: *Kingstonia trapezoidia*. Thin-bedded limestone interfingers 12.76	4.6	74.2
12.74–12.70	Alternating beds of massive limestone and thin-bedded limestone and shale. The lower portion of bed 12.72, coarse-grained granular limestone facies	5.1	69.6
12.69	*Cryptozoon undulatum* (with concentric rings ½–1 inch in diameter); a ⅝ inch shale facies occurs in lower portion of bed	0.3	64.5
12.68–12.67	Granular sandy limestone; edgewise conglomerate facies; thin-bedded limestone; lower 8¾ inches thin-bedded shales more predominant than limestone. Upper portion of bed arched downward	2.1	64.2
12.66	Massive limestone grading from fine- to coarse-grained sandy limestone; somewhat granular limestone is fossiliferous: *Lingulepis acuminata, Kingstonia apion, Coosia* sp., *Kingstonia trapezoidia, Genevievella? pennstatensis*. Lowermost part of bed interfingers with 12.65 and contains an edgewise conglomerate facies	2.9	62.1
12.65–12.63	Thin-bedded limestone and shales alternating with one massive limestone bed	3.2	59.2
12.62	*Cryptozoon undulatum* (with concentric rings ¼ inch in diameter)	0.7	56.0
12.61	Goarse-grained granular limestone, fossiliferous, resembles bed 12.57; edgewise conglomerate facies. About the twenty-fifth inch above the bottom of this bed, there occurs a four-inch facies of thin-bedded limestone and shale. *Kingstonia ara, Ithycephalus* sp., *Coosella convexa*	2.8	55.3
12.60	Thin-bedded limestone and shale	0.5	52.5
12.59	*Cryptozoon undulatum*. Lower portion of reef-facies interfingers 1½ inch black oolitic limestone facies	0.7	52.0
12.58	Massive limestone, sericite faced	0.7	51.3
12.57	Very coarse grained fossiliferous limestone: *Lingulepis acuminata, Genevievella campbellina, Kingstonia apion, Ankoura* cf. *orbiculata, Coosella* sp. no. 2	0.4	50.6
12.56–12.55	Sandy, coarse-grained limestone (6½ inches thick) interfingers less sandy fossiliferous limestone; a 3½ inch edgewise conglomerate facies. Undetermined trilobite fragments	0.8	50.2
12.54–12.50	Alternating thin-bedded and massive limestone; 12.52 concealed (1.1 feet), 12.51, sandy, coarse grained limestone	4.5	49.4
12.49	*Cryptozoon undulatum* (with concentric rings ⅜ inch in diameter)	0.2	44.9

	Thickness in Feet	
	Bed	Total
12.48–12.46 Alternating thin-bedded limestone and shale and massive limestone. 12.47 interfingers an oolitic limestone facies	1.1	44.7
12.45 Coarse-grained limestone interfingers black oolitic limestone facies. Upper 3½ inches fossiliferous: *Coosella convexa magnalimbata, Ankoura apicalis, Micromitra alabamensis, Kingstonia apion, Coosella convexa, Coosella* sp. no. 2, *Lonchocephalus planus*	0.7	43.6
12.44 Thin-bedded limestone and shale, sericite facing. Lower portion only is facies between beds 12.43 and 12.45	0.3	42.9
12.43 *Cryptozoon undulatum* interfingers bed 12.45, a black oolitic limestone facies; lower portion of this bed is a black oolitic limestone facies	0.7	42.6
12.42–12.40 Coarse-grained limestone; edgewise conglomerate facies; thin-bedded limestone and shale with sericite facing; massive limestone	2.2	41.9
12.39 *Cryptozoon undulatum* (with concentric rings ¼ inch in diameter)	2.1	39.7
12.38 Thin-bedded limestone, upper three inches, massive limestone	1.0	37.6
12.37 Massive limestone, upper seven inches, granular limestone, fossiliferous: *Coosella* sp. no. 2	1.6	36.6
12.36 Thin-bedded limestone	0.2	35.0
12.35 Massive limestone, upper part, *Cryptozoon undulatum*	0.7	34.8
12.34–12.23 Alternating beds of thin-bedded limestone and massive limestone, some sandy limestone, and bed 12.26 is an edgewise conglomerate facies	17.0	34.1
12.22 Covered	1.0	17.1
12.21–12.17 Thin-bedded sandy limestone. Bed 12.19, massive limestone	3.6	16.1
12.16 Oolitic limestone facies, and coarse, sandy limestone interfingers bed 12.15. First two inches fossiliferous: *Coosella convexa*	0.2	12.5
12.15–12.10 Thin-bedded, coarse- grained limestone and sandy shale, to coarse-grained sandy limestone; black oolitic limestone facies goes from finer to coarser oolitic; sandy interior; massive limestone deeply weathered, upper ¼ inch brown sand	4.2	12.3
12.9 Coarse-grained granular limestone, a facies of 12.8. *Coosella convexa, Lonchocephalus planus, Lingulepis acuminata*	0.4	8.1
12.8–12.6 Massive to sandy coarse-grained limestone	2.6	7.7
12.5 Covered	0.2	5.1
12.4 Massive limestone; first three inches interfingers 12.3	0.7	4.9
12.3 Sandy granular limestone. Upper 2½ inches fossiliferous: *Kingstonia trapezoidia, Kingstonia apion, Coosella convexa*	0.7	4.2
12.2 Covered	2.4	3.5
12.1 Massive limestone (Base 0.3 mile southeast of Waddle Road)	1.1	1.1
12.0 Covered interval		153.2±
11.41 Covered	22.5	93.9±
11.40 Coarse- to fine-grained massive limestone	3.7	71.4
11.39 *Cryptozoon undulatum*	0.7	67.7
11.38 A ten-inch thick, slumped massive limestone bed overlies *Cryptozoon undulatum* (3.5 inches thick)	1.1	67.0
11.37–11.35 Alternating massive limestone and thin-bedded shaly limestone	2.4	65.9
11.34 *Cryptozoon undulatum*	0.3	63.5
11.33 Massive limestone	0.4	63.2
11.32 *Cryptozoon undulatum*	0.3	62.8
11.31–11.13 Alternating beds of thin-bedded shaly limestone to fine and coarse-grained massive dolomite (Bed 11.13 sandy dolomite)	37.3	62.5
11.12 Massive limestone; first 18 inches fossiliferous: *Lonchocephalus planus, Genevievella campbellina, Ankoura* cf. *orbiculata, Kingstonia walcotti, Kingstonia ulrichi, Llanoaspis* (?) sp., *Kingstonia apion, Lingulepis acuminata*	3.7	25.2
11.11–11.2 Thin-bedded shale and limestone; alternates with massive dolomite. Bed 11.6, sandy facies in lower portion	19.4	21.5
11.1 Fine- to coarse-grained dolomitic limestone; following first 12 inches, an edgewise conglomerate facies (one inch thick) occurs; weathers sandy. (Base 0.2 mile southeast of Waddle Road)	2.1	2.1
Total Warrior Formation exposed directly on Highway #322		746.6±

occur, and to place, as precisely as possible, the exact position of the Warrior fossils. The essential constancy of dip and strike across the belt indicates a normal stratigraphic sequence.

THE WARRIOR FORMATION

Butts (1918, pp. 523–537) named the Warrior limestone formation from Warriors Creek in the northern part of Huntingdon County, east of Warriorsmark, Pennsylvania where a section totaling 1,250 feet in thickness occurs, and occupies the stratigraphic interval between the Middle Cambrian Pleasant Hill limestone below, and the Gatesburg formation above. The formation was originally described as "thick and thin-bedded blue limestone with thin, siliceous, shaly layers or partings. A few thin quartzite layers and an occasional bed of limestone full of well-rounded quartz grains. Some oolite. Cryptozoon common. Several species of trilobites" (Butts, 1918). As redescribed later (Butts, 1939), the formation is "composed of interbedded limestone and dolomite, with thin layers of siliceous shale or shaly limestone." Trilobites from that locality, collected by Butts, are numbered 24-g and 24-f.

Warrior exposures at two other localities were measured by Butts. In a section north-northwest of Scotia in the Bellefonte Quadrangle, the upper part of the formation is formed by some 688′ of dense, thick to thin-bedded, blue to dark-blue limestone with layers of edgewise conglomerate and shaly partings, oolitic limestone and reef-like *Cryptozoon undulatum* beds. Unidentified trilobite fragments were reported from compact limestone beds 202 feet and oolitic limestone 378 feet below the top of the section (Butts, 1936, p. 13). Another section of the Warrior limestone on the Frankstown Branch midway between Williamsburg and Ganister, Huntingdon Quadrangle, some 1,251 feet thick, consists largely of dolomite but includes considerable pure limestone, some thin quartzite beds, and layers full of rounded quartz (Butts, 1945, p. 2). Unidentified trilobites were reported 200 feet below the top of this section which is overlain by the Stacy dolomite member of the Gatesburg formation.

The Warrior limestone surfacing in Friend's Cove, Everett Quadrangle, is some 1,200 feet thick and is overlain by the Gatesburg sandy dolomite. It includes "dark, medium textured, in part oolitic limestone bearing diagnostic Upper Cambrian trilobites. Thin *Cryptozoon* reef beds and argillaceous limestones also are present" (Swartz 1948a, p. 113; chart 3, p. 115). In the vicinity of Friend's Cove, Swartz observes "the Warrior limestone contains silty and shaly layers, together with two local, thin layers of quartz sandstone; the lower part of the Pleasant Hill limestone is shaly. The direction from which these detritals were derived remains uncertain; the quartz sand lenses of the Warrior could have been reworked from uparched, emergent portions of the Lower Cambrian sandstones" (1948a, p. 114). A new trilobite species from this locality, *Lonchocephalus swartzi* is described in the present study.

Krynine (1946, p. 2) reported the results of a petrographic study of the Warrior limestone exposure three-tenths of a mile south of the Waddle Road on Highway Number 322 as follows: "Carries a considerable amount of volcanic ash which is distributed at least through 200 feet of the Warrior and possibly more. The insoluble residue which forms 2.7 percent of the rock carried a large amount of the hexagonal biotite flakes (partly altered to chlorite), good apatite crystals and apparently a hypersthenelike (?) mineral. There are no well-defined bentonites in the Warrior and the volcanic material is hidden throughout the limestone."

Upper Warrior sedimentation is clearly "cyclical" and Krynine gave the following phases as probably representative of "a fairly typical cycle:"

Phase		Feet
1	*Cryptozoon*	1–2
2	Massive black limestone (possibly part of the *Croptozoon* reef)	1–2
3	Thin bedded limestone	3–5

Field observations made during the present investigation show that (1) only one measured reef-facies was two feet thick, while in general, maximum thickness for such facies was less than one foot; (2) in the second phase, the massive black limestone is frequently oolitic; (3) in the third phase, silty and shaly layers, as well as

thin-bedded limestones, recur, as do edgewise conglomerate facies.

Edgewise conglomerate facies largely occur as thin, smooth and flat, lath-like slivers, generally with a common orientation, and held together in a limey matrix. While their recurrence is noteworthy, they constitute a negligible portion of the total volume of sediments.

THE WARRIOR FAUNA AND ITS OCCURRENCE

The assemblage of fossils discovered in the Warrior formation and described up to the present time, consists of the following:

Algae:	one species
Trilobites:	19 genera, 40 species, three varieties
Brachiopods:	four genera, four species
Pteropods:	number of species undetermined

Of the trilobites, one genus, 24 species, and three varieties are newly described in the present paper. The species now known from the Warrior formation are named in the following list. In addition, species previously recognized by other workers are included. These have been starred for ready indentification. A double star signifies species previously recognized and included in the present collections. Single star signifies species previously recognized and not included in the present collection.

ALGAE

***Cryptozoon undulatum* Bassler

BRACHIOPODS

Acrotreta sp. undet.
Lingulella cf. *marcia* Walcott
Lingulepis acuminata (Conrad)
Micromitra alabamensis (Walcott)

PTEROPODS

Hyolithes sp.

TRILOBITES

Ankoura apicalis Duncan
Ankoura sublettensis (Miller)
Ankoura cf. *orbiculata* Lochman

EXPLANATION OF PLATE 44

FIGS. *1, 2—Ankoura apicalis* Duncan. Plesiotype, dorsal and side views of a peeled pygidium, ×2¼, USNM 115592, loc. 24-f. (p. 286)

3, 4—Ankoura sublettensis (Miller). Plesiotype, dorsal and side views of a pygidium, ×2¼, USNM 115593, loc. 24-f. (p. 286)

5—Genevievella plesiochielus Tasch, n. sp. Holotype, dorsal view of pygidium, ×2¼, USNM 115637, loc. 24-e. (p. 293)

6, 16, 17—Kingstonia walcotti Resser. *6*, Plesiotype, side side view of cranidium, ×2, USNM 115600, loc. 24-f; *16, 17*, Plesiotype, dorsal and side views of pygidium, ×3¾, USNM 115600, loc. 24-f. (p. 298)

7—Genevievella (?) *pennstatensis* Tasch, n. sp. Holotype, dorsal view of cranidium, ×5, USNM 115641, loc. 24-d. (p. 293)

8–10—Kingstonia trapezoidia Tasch, n. sp. *10*, Holotype, dorsal view of cranidium and free cheek, ×3½, USNM 115601, loc. 24-f; *8, 9*, Paratype, side and frontal view of cranidium, ×3½, USNM 115602, loc. 24-f. (p. 296)

11, 12—Hallaspis matutina (Hall). Plesiotype, dorsal and side view of cranidium showing narrow brim, ×2¾, USNM 115628, loc. 24-b. (p. 294)

13—Pemphigaspis bullata waddlensis Tasch, n. var. Holotype, dorsal view of pygidium, ×3, USNM 115629, loc. Old Quarry three-fourths of a mile south of Waddle crossroads. (p. 302)

14, 15—Llanoaspidella bigenusia Tasch, n. gen., n. sp. Holotype, dorsal and side views of cranidium showing presence of complete occipital furrow and occipital lobe connectives to glabella, ×3, USNM 115635, loc. Bellefonte Quad. 7285. (p. 299)

18–20—Kingstonia ulrichi Tasch, n. sp. *18, 19*, Syntype, dorsal and side views of long pygidium, ×1½, USNM 115595a, loc. 24-d; *20*, syntype, dorsal view of cranidium found associated with short pygidium, ×2¾ USNM 115696, 115595b, loc. 12.79. (p. 297)

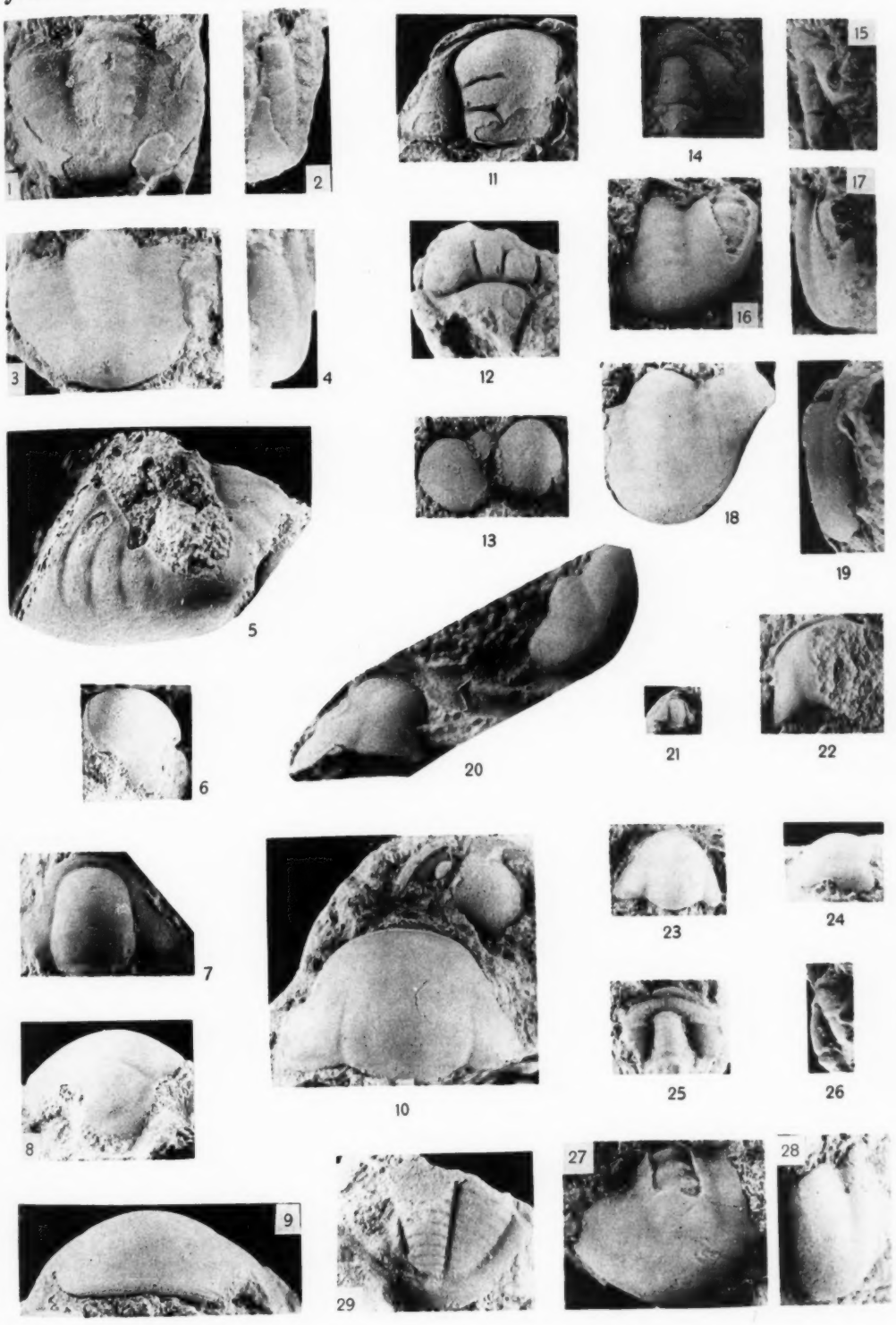
21—Ithycephalus sp. undet. Dorsal view of cranidium, ×2¾ USNM 115642, loc. 24-f. (p. 295)

22—Ankoura cf. *orbiculata* Lochman. Dorsal view of poorly preserved cranidium, ×2, USNM 115594, loc. 11.12. (p. 286)

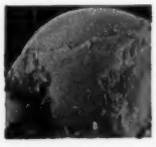
23, 24, 27, 28—Kingstonia apion Walcott. *23, 24*, Plesiotype, dorsal and side views of cranidium, ×1¼, USNM 115598, loc. 24-f, 24-b; *27, 28*, plesiotype, dorsal and side views of a pygidium, ×3¾, USNM 115599, loc. 24-f, 24-b. (p. 295)

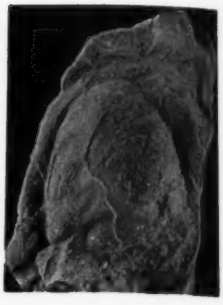
25, 26—Holcacephalus tunda atypicala Tasch, n. var. Holotype, dorsal and side view of cranidium ×2¼, USNM 115636, loc. 24-d. (p. 294)

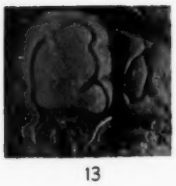
29—Blountia warriorensis Tasch, n. sp. Holotype, dorsal view of pygidium, ×2¼, USNM 115605, loc. 24-d. (p. 287)

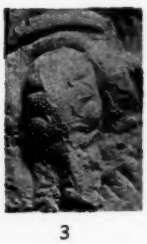
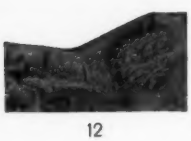


Tasch, Cambrian Warrior limestone fauna







Tasch, Cambrian Warrior limestone fauna

Blountia kindlei Resser
Blountia prolifica Tasch, n. sp.
Blountia waddlensis Tasch, n. sp.
Blountia warriorensis Tasch, n. sp.
Blountia sp. undet. 1
Bonneterrina aspinosa Tasch, n. sp.
Coosella brevis Resser
Coosella convexa Tasch, n. sp.
Coosella convexa magnalimbata Tasch, n. var.
Coosella aff. *convexa* Tasch
Coosella vulgaris Tasch, n. sp.
Coosella sp. undet. 1
Coosella sp. undet. 2
Coosia ? pustulata Tasch, n. sp.
Crepicephalus sp. undet. 1
Genevievella campbellina Tasch, n. sp.
Genevievella ? pennstatensis Tasch, n. sp.
Genevievella plesiochielus Tasch, n. sp.
Hallaspis matutina (Hall)
Holcacephalus tunda atypicala Tasch, n. var.
Ithycephalus sp. undet.
Kingstonia apion Walcott
**Kingstonia ara* (Walcott)
Kingstonia cheilusis Tasch, n. sp.
**Kingstonia kindlei* Resser
Kingstonia trapezoidia Tasch, n. sp.
Kingstonia ulrichi Tasch, n. sp.
Kingstonia walcotti Resser
Llanoaspidella bigenusia Tasch, n. sp.
Llanoaspidella warriorsmarkensis Tasch, n. gen., n. sp.
Lonchocephalus planus Tasch, n. sp.
Lonchocephalus swartzi Tasch, n. sp.
Lonchocephalus waddlei Tasch, n. sp.
Menomonia calymenoides (Whitfield)
**Millardia avitas* Walcott
Modocia benorensis Tasch, n. sp.
***Pemphigaspis bullata waddlensis* Tasch, n. var.
Pemphigaspis intermedia Tasch, n. sp.
Tricrepicephalus arcuatus Tasch, n. sp.
Welleraspis cf. *newfoundlandensis* Lochman

The reported arrangement of some of the above trilobite species in the Warrior formation at the type locality and the observed arrangement in the section measured by the writer are indicated below. Trilobite species belonging to key genera or to genera often associated with them in the same faunal zone are grouped into the *Cedaria* zone fauna or *Crepicephalus* zone fauna. Such groupings are intended to be indicative rather than definitive and are based on faunal relationships reported to hold consistently in Upper Cambrian formations elsewhere in the United States. "Key" genera of these zones are starred.

EXPLANATION OF PLATE 45

FIGS. *1–3*—*Lonchocephalus waddlei* Tasch, n. sp. *3*, Holotype, dorsal view of partly exfoliated cranidium, ×1½, USNM 115612, loc. 24-b; *1*, *2*, paratype, dorsal and side view of cranidium, ×3, USNM 115613, loc. 24-b. (p. 300)

4, *5*—*Kingstonia ara* (Walcott). Plesiotype, dorsal and side view of cranidium, ×2¾, USNM 115603, loc. 24-b. (p. 295)

6—*Micromitra alabamensis* (Walcott). Plesiotype, ventral valve showing crenulation of striae, ×4¼, USNM 115624, loc. 24-d. (p. 304)

7—*Lingulella* cf. *marcia* Walcott. Partly exfoliated dorsal valve, ×3½, USNM 115625, loc. 24-d. (p. 304)

8—*Acrotreta* sp. undet. Well preserved conical ventral valve, ×2¾, USNM 115626, loc. 24-b. (p. 303)

9–12—*Tricrepicephalus arcuatus* Tasch, n. sp. *9*, *10*, Holotype, dorsal and side views of cranidium, ×2; *11*, *12*, holotype, dorsal and side views of pygidium showing features of the pygidial spine, ×2, USNM 115623, loc. 13.3. (p. 302)

13—*Welleraspis* cf. *newfoundlandensis* Lochman. Partly preserved exfoliated cranidium, ×2¾, USNM 115647, loc. 24-h. (p. 303)

14—*Coosella* sp. undet. 1. Dorsal view of cranidium, ×1¼, USNM 115618, loc. 24-b. (p. 291)

15—*Kingstonia cheilusis* Tasch, n. sp. Holotype, dorsal view of cranidium, ×3½, USNM 115597, loc. 24-f. (p. 296)

16, *17*—*Lonchocephalus swartzi* Tasch, n. sp. *16*, Holotype, dorsal view of cranidium partly concealing dorsal view of pygidium, ×3½; *17*, holotype, side view of cranidium showing characteristic occipital spine, ×3½, USNM 115611, loc. Friend's Cove, half a mile northeast of Hartley, Pennsylvania. (p. 300)

18—*Lingulepis acuminata* (Conrad). Plesiotype, narrow form of ventral valve, ×1½, USNM 115627, loc. 24-d. (p. 304)

19, *20*—*Coosella vulgaris* Tasch, n. sp. *20*, Holotype, dorsal view of cranidium, ×2¼, USNM 115616, loc. 24-h; *19*, paratype, side view of cranidium, ×2, USNM 115617, loc. 24-b. (p. 290)

Warriorsmark Section—Type Locality
(measured by Butts)
Thickness 1,250 feet

Loc. 24-f, Upper third of formation
**Ankoura apicalis*
**Ankoura sublettensis*
**Genevievella campbellina*
Bonneterrina aspinosa
Kingstonia ara

No fossils from middle part of section

Loc. 24-g, Lower part of formation

Llanoaspidella warriorsmarkensis

Exposure on Highway Number 322
near Road to Waddle
(measured by Tasch)
Thickness 746.6 ± feet

Bed	
13.9	*Blountia prolifica*
13.3	*Blountia prolifica*
	Coosia? pustulata
	Tricrepicephalus arcuatus
13.2	*Coosia? pustulata*
	**Crepicephalus* sp. no. 1
12.97	*Blountia prolifica*
12.66	**Genevievella pennstatensis*
12.61	*Kingstonia ara*
12.57	**Genevievella campbellina*
	**Ankoura* cf. *orbiculata*
12.45	**Ankoura apicalis*
?	*Llanoaspidella bigenusia*
11.12	**Genevievella campbellina*
	**Ankoura* cf. *orbiculata*
	**Llanoaspis?*

STRATIGRAPHY

A consideration of some importance in completing the above picture is the stratigraphic position occupied by Warrior rocks exposed in the Old Quarry, three-fourths of a mile south of Waddle, and off a short distance from Highway Number 322. There are two alternatives, among others, that may explain the stratigraphic position of these rocks.

Either they lie below the base of exposure number 11, or, occurring as they do in the vicinity of the Birmingham fault, these rocks may only appear to lie below the base of exposure number 11, with their present position accounted for by faulting. The present collections have yielded *Pemphigaspis bullata waddlensis* from rocks of the Old Quarry and some other, as yet unidentified, trilobite specimens.

A comparison of the section measured by Butts and that measured by the writer brings out some interesting relationships. The Warriorsmark section (Loc. 24-f) contains an apparent *Cedaria* fauna which corresponds with a *Cedaria* fauna of the section near Waddle. Three of the same species occur at both localities: *Ankoura apicalis*, *Genevievella campbellina*, *Kingstonia ara*. Above bed 12.97 in the section near Waddle, there occurs a *Crepicephalus* fauna. Thus, at this locality, the uppermost beds contain *Crepicephalus* and immediately below, occurs a *Cedaria* fauna. The same new genus, *Llanoaspidella*, which bears closest affinities to *Llanoaspis*, is represented at both localities by different species.

A series of apparent anomalies arise as one studies the faunal associations and tries to accommodate them to the *Cedaria* and *Crepicephalus* zones. *Pemphigaspis*, a "key" genus of the *Crepicephalus* zone, comes from rocks of the Old Quarry, If, as already stated, these rocks are actually below the base of exposure number 11, this may indicate a *Crepicephalus* zone fauna occurring below a *Cedaria* zone fauna. On the other hand, locality 7341, where rocks of the same age as those of exposure number 13 occur, has also yielded a *Pemphigaspis* species, *P. intermedia*. Since other *Crepicephalus* zone forms have been collected by the writer in exposure number 13, this may favor the second alternative for the rocks of the Old Quarry, namely faulting. The data of the present study, while suggestive, are insufficient to solve this problem.

Another problem that arises concerns the new genus, *Llanoaspidella*. Does it belong to the *Crepicephalus* or to the *Cedaria* zone? Conceivably, it may be a precursor of *Llanoaspis*. If so, its reported occurrence in the lower part of the Warriorsmark section and in the section near Waddle with a *Cedaria* fauna, may indicate that the lower part of the Warriorsmark section, as well as the upper, is in the *Cedaria* zone. It would then follow that the *Crepicephalus* zone in the

upper one hundred feet of section near Waddle (exposure number 13) probably pinches out towards Warriorsmark. If the alternative proves to be true, namely, that *Llanoaspidella* is a *Crepicephalus* zone form, the anomalous occurrence of this zone at Warriorsmark would parallel a similar occurrence in the section near Waddle, if the rocks of the Old Quarry are stratigraphically below the base of exposure number 11.

The occurrence of only a single genus in the available material from both the Old Quarry and the lower part of the Warriorsmark section, hampers the solution of the problem at present. What can be said with some degree of certainty at this time, is that the section measured by the writer has a clearly defined *Crepicephalus* zone above bed 12.97. Species of *Ankoura*, *Genevievella* and *Kingstonia walcotti*, prominent in several earlier horizons, do not occur in any of the fossiliferous beds of exposure number 13. This, and similar evidence, indicates that below bed 12.97 a *Cedaria* fauna occurs.

Interregional Correlations.—Many of the species of trilobites occurring in the Warrior formation together with close relatives and additional forms have been reported from the Upper Cambrian Cap Mountain formation of Texas, the Cow Head breccia of western Newfoundland, the Eau Claire sandstone formation of Wisconsin, the Bonneterre dolomite of Missouri, the Pilgrim limestone formation of Montana, the Nolichucky shale, and the Conasauga formation of the southern Appalachians, and in a more limited sense, in the *Tricrepicephalus* zone of the Nevada-California area (Mason, 1938, pp. 288–292).

Butts (1936, p. 14) provisionally correlated the upper half of the Warrior limestone with the lower part of the Eau Claire formation of Wisconsin and with the Nolichucky shale of the southern Appalachians. In 1940 he suggested that the upper part of the Elbrook formation might be of Warrior age.

Bassler (1919, p. 78) noted that the Conococheague limestone in the Hagerstown Valley, Maryland, had a "basal division of two hundred and fifty feet of oolite, edgewise conglomerate, and *Cryptozoon* reefs." The section studied by the writer is characterized by similar lithology. Comparable lithology might be suggestive of possible age equivalence between the upper Warrior and basal Conococheague. However, unsupported by faunal evidence, nothing conclusive could be said about the correlation of the two formations. Such evidence was recently forthcoming and both of the above correlations were confirmed (Wilson, 1949, p. 14).

COMPOSITION AND ECOLOGY OF THE WARRIOR FAUNA

Warrior Biota.—In the present collections the largest number of fossils are trilobite molt fragments. These are represented by 19 genera, 40 species, and three varieties. No Warrior trilobites are represented by complete exoskeletons. Blue-green algae probably occurred in great numbers as indicated by the cyclical occurrence of *Cryptozoon* reef-facies in upper Warrior time.

A relatively large number of trilobite genera and species occur in the upper part of the Warrior formation. This diversity, in itself, may serve as a climatic indicator, and allows inferences to be drawn about the probable salinity of the upper Warrior seas.

Thus, studies of modern warm and cold water faunas indicate that the warm waters of the equatorial belt "are rich in genera and species but have a smaller number of individuals per species than are found elsewhere" i.e., in colder waters (Hesse, Allee, and Schmidt. 1937, p. 272). Although this great diversity in species in tropical waters has been particularly noted among pelagic animal communities, it has application to fossil marine invertebrate benthos as well. Further indication that this is so comes from two lines of evidence other than diversity of trilobite genera and species. These are the occurrence in the upper Warrior of *Cryptozoon* reef-facies and oolites.

(1) As later discussion will develop, calcareous algae flourish in warm waters and the cyclical occurrence of *Cryptozoon* reef-facies indicate warm water at such times. (2) In the period between reef-facies, and occasionally contemporaneous with individual facies, oolitic limestone was deposited. "Modern oolites are most abundant in warmer latitudes" even though they occur in temperate latitutes and "some hot weather seems to be a favoring factor" (Twenho-

fel, 1932, p. 769; Stetson, 1938, p. 26).

Items one and two above, allow the inference to be made that the shallow seas of middle to late Warrior time were warm water; while study of modern marine faunas suggests that such warmness favored the observed diversity of Warrior trilobite species and genera.

Diversity of trilobite species and the small size of fossilized cranidia and pygidia are maintained more or less uniformly in upper Warrior beds represented in the present collections. It has been suggested that, working along a given "marine horizon" should one find that (a) the number of species of animals increases, and (b) that the average size of fossil animals increases, "it is strong evidence that he is following a former salinity gradient" (Gunter, 1947, p. 76). Interpreted in light of this observation, the effective constancy in both diversity of number of species and in average size, may indicate relatively uniform salinity in the shallow seas that covered the area involved.

The arched or pointed frontal border of the cranidium (*Tricrepicephalus*) and the prominent pygidial spines (*Tricrepicephalus, Crepicephalus*) suggest that these characters are adaptive modifications of active crawling forms. The absence of these characters, together with the occurrence of the smooth, convex cranidia and smooth, spineless pygidia of the kingstonid trilobites (*Kingstonia, Ankoura*) have been interpreted as indicating adaptation of burrowing forms (Lochman, 1940, p. 7).

The kingstonid trilobites were the most numerous component of the total trilobite population insofar as that population may be inferred by the numbers of fossils of the different genera represented in the present collections. In contrast, crepicephalid trilobites, the active crawling forms, were relatively sparse in the late Warrior seas. Next to the kingstonid trilobites, species of the genus *Coosella* were apparently most numerous.

However abundant brachiopods were in Upper Cambrian Warrior seas, their preservation as fossils was extremely rare. *Micromitra* and *Lingulepis*, represented by a very few individuals, occurred between the times of deposition of certain reef-facies in association with kingstonid trilobites and *Coosella*. Single specimens of *Acrotreta* and *Lingulella* were found near the top of the Warrior. Since lingulid brachiopods inhabited the shore zone, living close to shore (Cooper, 1937, p. 34), their occurrence at times between reef-facies deposition provides additional evidence of the shallowness of water then prevailing.

The pteropod, *Hyolithes*, occurs sparsely throughout the formation with the exception of locality 24-b where it is found in abundance in association with several species of kingstonid trilobites. One may be reasonably certain, in light of the evidence given above, that the presence of this pelagic form in the upper Warrior cannot be interpreted as indication of deeper water.

Reconstruction of the Marine Environment of Upper Warrior Time.—As a basis for a plausible reconstruction of the marine environment of late Warrior time, we shall consider separately times when reef-facies were deposited and times represented by beds occurring between any two reef-facies.

Times of Reef-facies Deposition

Modern calcareous algae, important as reef-builders, such as *Lithothamnium* and *Halimeda* are generally reported to occur in greatest profusion in well lighted marine water (euphotic zone) of very shallow depths (Goldring, 1938, pp. 52, 54–55; Glock, 1946, pp. 279–281; Tracey, Ladd, Hoffmeister, 1948, pp. 861–878; Emery, 1948, pp. 855–860). While it may be observed that calcareous algae "probably played as important a role in the construction of ancient reefs" (Shimer and Shrock, 1947, p. 716) as in the building of modern coral reefs, the distinction should be made between fossil coral and *Cryptozoon* reefs found in the geologic column. Reefs built by algae assignable to the genus *Cryptozoon* were apparently built solely by blue-green algae by deposition of calcium carbonate "as crusts on the outside colony or cell, or between tissues." This distinction is of some importance since where coral reefs are being built today at depths greater than five to six fathoms, corals are the more important reef-builders, while above

that depth, calcareous algae play the larger role (Pettijohn, 1949, p. 295).

Cryptozoon undulatum Bassler "apparently began as an undulant, mammillose laminae which spread in sheets upon lime mud bottoms. Above this basal zone, colonies break into distinct or confluent domes or columns . . . (some columns) indicate *cessation of growth with deposition of sediment*, followed by growth of new domes" (Fenton and Fenton, 1937, p. 437, italics mine). Glock's conclusion that clear and warm water are among the optimum conditions for growth, is supported by the observation of the Fentons on the possible influence of sedimentation on growth. In view of these considerations, and bearing in mind that *Cryptozoon* occurrence in the upper Warrior seas was cyclical, we can interpret the beds occurring between any two reef-facies as representing times of turbid waters which were inimical to algal growth.

Times Between Reef-Facies Deposition

In the Warrior section measured by the writer, edgewise conglomerates and oolites were found to recur along with reef-facies. Such edgewise conglomerates have been interpreted as being formed when the edges of mud cracks on a tidal flat curl up and are broken off. They are then tossed about by wind or rising tidal waters, finally coming to rest in a limey mud matrix on the sea floor (Bassler, 1919, p. 78). The writer favors the interpretation that rising tidal water rather than wind caused the movement of the curled mud slivers, in the present occurrence.

Warrior oolites are most probably of shallow water origin. Since the depths at which oolites form have not been determined (Twenhofel, 1932, p. 767), this conclusion is far from being an obvious one. Two lines of evidence in support of it can be cited. First, since Warrior oolites occasionally interfinger reef-facies (Beds 12.59; 12.45) which, as shown earlier, are most likely of shallow water origin, it is reasonable to assume that these oolites also have this origin. Second, study of recent sediments show that "oolites from the offshore samples are largely white and ivory colored, whereas those from shallower waters are usually black. Both varieties have a concentric structure around a quartz nucleus" (Stetson, 1938, p. 25). Warrior oolites are of the black variety and show both radial and concentric structures cemented by carbonate (Pettijohn, 1949, Plate 2, figure B; Plate 26, figure E). Since it is unlikely that present bottom conditions are favorable to oolite formation (Stetson, 1938, p. 29), the oolites described above probably have been derived from some older formation (idem, p. 23). This raises the question as to whether the older formation was laid down in shallower waters. In terms of the modern distribution of black and white oolites, there is at least a fair likelihood that black oolites were originally laid down in shallower waters. If this is true, the black oolites of the Warrior may be assumed to have been laid down in water of similar shallow depth.

Oolitic beds are commonly fossiliferous, consisting of well-sorted trilobite fragments largely belonging to kingstonid trilobites. The persistence of kingstonid trilobites during the times that elapsed between deposition of successive *Cryptozoon* reef-facies and the relatively sparse occurrence of other genera (with the exception of *Coosella*) is of more than usual interest. This is so because such beds represent times when excessive shallowing of water occurred as shown above. At such times, therefore, it is reasonable to assume that trilobites of burrowing habit were better able to survive.

Thus, general reconstruction of the marine environment of upper Warrior time, leads to the hypothesis that the sediments and faunas reflect a cycle of alternations between three different environments, namely, a *Cryptozoon* reef environment characterized by clear, warm, shallow water, an environment of turbid waters in which either clay or finely flocculated lime came to rest on the sea floor, and choked off algal growth, and an environment of exposure and covering of tidal flats. Fossils from the upper Warrior beds described in this paper may be viewed as representing forms that lived in this kind of variable marine environment.

SYSTEMATIC DESCRIPTIONS

TRILOBITA

Genus ANKOURA Resser 1938

ANKOURA APICALIS Duncan

Plate 44, figures 1, 2

Ankoura apicalis DUNCAN, 1944, Geol. Soc. America Special Paper 54, p. 109, plate 14, figures 29–31.

Supplementary description.—Pygidia subtriangular to semicircular; axial lobe three-fourths length of pygidium, divided into four or six segments.

Remarks.—Few specimens in present collection, occurring at one locality. The critical specific feature is the "sharply rounded dorsal apex of pygidium." The following parts of the original description apply to many kingstonids and have no special value for *Ankoura*: inner surface of test finely punctate; axial width and length relative to pygidium as a whole is usually one-third to three-fourths respectively; axial segments will vary from four to six; dorsal furrows of pygidia will commonly vanish posteriorly; increase of width of narrow marginal border on posterior median line of pygidium is reported for *Kingstonia walcotti* for example, hence does not have unique value for *A. apicalis*.

Occurrence.—Loc. 24-f, 12.45.

Types.—Plesiotype, USNM 115592, loc. 24-f.

ANKOURA cf. ORBICULATA Lochman

Plate 44, figure 22

Remarks.—From two horizons several cranidia were collected which bear closest affinity to *Ankoura orbiculata* Lochman. They differ from *orbiculata* as follows: cranidia are more nearly trapezoidal, having shorter posterolateral limbs; glabella narrowly, instead of broadly, conical; brim and border narrower than in *orbiculata*. The small number of specimens and the partial nature of their preservation do not permit more accurate specific determination.

Occurrence.—Loc. 11.12, 12.57.

Figured specimen.—Cranidium, USNM 115594, loc. 11.12.

ANKOURA SUBLETTENSIS (Miller)

Plate 44, figures 3, 4

Kingstonia sublettensis MILLER, 1936, Jour. Paleontology, vol. 10, p. 31, pl. 8, figs. 28–29.
Ankoura sublettensis (Miller) LOCHMAN & DUNCAN, 1944, Geol. Soc. America Special Paper 54, p. 110, pl. 14, figs. 51–54.

Additional description.—Axial width to width of pygidium is slightly greater than one-third; similarly, axial length to length of pygidium is slightly greater than three-fourths.

Remarks.—Lochman and Duncan's supplementary description is more diagnostic of the pygidia of the species than Miller's original description.

In Resser's original description of the genus, "the swayback longitudinal outline of the axis which elevates the rear end" is a critical generic feature. *A. sublettensis* pygidia do not show this feature. In fact, one of the characters that make *sublettensis* a species, is its variance from this "unique" feature of *Ankoura* trilobites. Nevertheless, as in *A. apicalis* Duncan, where the "posterior end of the axial lobe is without a node but nevertheless strongly upholds the dorsal margin," *sublettensis* also has the generalized feature of an "elevated rear end" in the following variation: the profile "curves down more rapidly" beyond the marginal border.

Occurrence.—Few specimens at loc. 24-b, 24-f.

Types.—Plesiotype, USNM 115593, loc. 24-f.

Genus BLOUNTIA Walcott 1916

BLOUNTIA PROLIFICA Tasch, n. sp.

Plate 47, figures 2–4

Cranidium broad, with broadly conical, gently convex, smooth glabella; no glabellar furrows visible; dorsal furrow shallow and narrow, defines glabella on three sides; occipital furrow faint, defined along midpart only; occipital ring slightly rounded, narrower than occipital furrow. Posterolateral limbs about three-fifths the width of base of glabella, taper to broad pointed ends, broad intramarginal furrow that widens towards the extremities; fixed cheeks convex, about two-fifths width of the glabella; palpebral lobes not preserved; ocular ridge faint, runs from anterior outer side of dorsal furrow in curved diagonal across fixed cheek, indicates position of palpebral lobe in line through anterior third of glabella; brim convex, curving downward,

having same trend as anterior of glabella, anteriorly bordered by shallow marginal furrow; frontal border arcuate in outline, continues directly from anterior side of marginal furrow, slightly upthrust at angle of less than five degrees, flat, terminates in longitudinal striae-like, low, narrow ridges; frontal border and brim of about equal width. In profile view, anterior margin of border stands at a level barely above the posterior of the brim.

Pygidium smooth, variable between semicircular and semielliptical in outline; axial lobe narrow, slightly convex, tapered, merging posteriorly into slope of marginal border; eight to nine segments plus terminal portion; axis stands above pleura; pleura convex, about same width as axis; pleural furrows faint; separated from axis by shallow, narrow dorsal furrow and from border by shallow, marginal furrow; marginal border slightly convex, widens near terminus of axis which overlaps onto it; where axis and margin merge, a slightly concave curve is seen in lateral profile view.

Exfoliated cranidia bear small pustule-like knobs on surface of glabella.

Relationships.—*B. prolifica* resembles *B. nixonensis* in having a brim and frontal border of nearly equal width, but differs from it in the width of fixed cheek and in the non-obsolescence of dorsal and occipital furrows. *B. prolifica* differs from other described *Blountia* species in the following characters: width of posterior lateral limbs and blunt pointed extremities; curvature of frontal border.

Occurrence.—Cranidia and pygidia collected in relative abundance from several horizons near top of Warrior formation. Loc. 13.9, 13.3. 12.97.

Types.—Holotype cranidium and pygidium, USNM 115606, loc. 13.3; paratype cranidium, USNM 115607, loc. 13.3.

BLOUNTIA WADDLENSIS Tasch, n. sp.
Plate 46, figures 6–9

Cranidium semiovate, with gently convex glabella, broadly conical; dorsal furrow completely defines glabella; palpebral lobe situated on transverse median line of glabella; brim convex, marginal furrow broad, shallow; border variable from flat to slightly convex, terminating in horizontal ridges and furrows (striae); brim and border of equal width; fixed cheeks convex, about one-half width of glabella; posterolateral limbs convex, of less width than base of glabella; intramarginal furrow narrow, shallow. Exterior surface punctate. In lateral profile gentle convexity of glabella ends at dorsal furrow in front of anterior of glabella; from the furrow the brim continues convex downward to marginal furrow; border rises outward at low angle from the outer side of this furrow.

Associated pygidium smooth, almost uniform, gentle convexity in horizontal and vertical direction; surface of exterior punctate; axis flat, set off from pleural lobes by shallow, dorsal furrows that define it along its entire length, axis slightly elevated above furrows; merges with margin without any change in curvature beyond gentle descent from axial terminal node; twelve axial segments and terminal portion; pleural lobes convex, on the average slightly wider than axis along transverse median line. Margin wide, curved downward; same width along sides of pleural lobes and along base of axial lobe. Pleural lobes separated from margin by shallow marginal furrow and are thus defined by this furrow on the outside and the dorsal furrow on the inside.

Relationships.—*B. waddlensis* cranidia differ in lateral profile from all other described *Blountia* species. The pygidia most closely resemble those of *Blountia* sp. undet. no. 1, as hereafter described, but differ from them in the following ways: absence of concavity of the margin; extension of the terminal portion of the axial lobe slightly beyond the marginal furrow; larger number of axial segments.

Remarks.—In rocks of the same lithology at loc. 25-g, cranidia and pygidia of *waddlensis* are found separately. The pygidia are tentatively assigned to *waddlensis*.

Occurrence.—Loc. 25-g, 24-d, 107-k.

Types.—Holotype cranidium, and tentatively assigned pygidium, USNM 115604, loc. 25-g.

BLOUNTIA WARRIORENSIS Tasch, n. sp.
Plate 44, figure 29

Cranidium small with broadly conical glabella of gentle convexity in vertical and horizontal directions. Holotype glabella 3.8

mm. wide along base; gently rounded in front; no glabellar furrows; brim concave; border not preserved. Dorsal furrows shallow. Fixed cheeks greater than one-half width of glabella. Posterolateral limbs convex, large, slightly wider than the base of the glabella. Intramarginal furrow vanishes midway beyond the dorsal furrow and posterolateral limb extremity; area above intramarginal furrow inflated.

Thorax and free cheeks unknown.

Pygidium semiovate in outline; axis gently convex, extending two-thirds the length of the pygidium; contains seven or more segments; tapers posteriorly; axis paralleled along entire length by shallow furrows on either side of it. Pleural lobes low, convex, smooth in appearance but when held at oblique angle in light show faint segmentation, seven segments; slightly wider than axis, margined by shallow furrow that runs below last axial segment; border convex, of equal width along entire extent.

Relationships.—The pygidium has closest affinities to *B. cora* but differs from it in having pleural lobes that are wider than the axial lobe, and the axial lobe does not merge with the border without a slight change in direction.

Remarks.—The holotype cranidium is poorly preserved but the critical feature is the elongate posterolateral limbs and concave brim.

Occurrence.—Loc. 24-d.

Types.—Holotype cranidium and pygidium, USNM 115605, loc. 24-d.

BLOUNTIA sp. undet. 1
Plate 47, figures 5, 6, 21

Pygidium smooth, surface of exterior punctate; axis convex, tapers posteriorly, terminal portion does not extend beyond furrow defining axial node, two-thirds length of pygidium, shows seven faintly marked segments and terminal portion. Pleural lobes low, convex, wider than axial lobe. Dorsal furrows shallow, spread out into "V" shape along sides of axis; wide margin curved slightly downward. In side profile, the margin gently curves downward from the node-like terminal portion of the axis; this curvature has slight concavity.

Free cheek punctate, border bearing vertical striations on periphery, ends in broad genal spine; wide marginal furrow separates concave ocular platform from border. Bean-shaped eye, small, punctate, on inside of ocular platform.

Facial suture must have cut border well out to side, proceeded inward and downward to marginal furrow, then, following almost a straight line, continued inward and downward within genal angle.

Cranidium and thorax unknown.

Remarks.—The material available is too sparse to permit specific identification. However, study of other *Blountia* species in the collection and those previously described, suggests that the present unassigned *Blountia* material probably belongs to a distinct species.

Occurrence.—Rare in present collection. Old Quarry near Waddle, Pa.

Figured specimens.—Pygidium and free cheek, USNM 115608, Old Quarry near Waddle.

Genus BONNETERRINA Lochman 1936
BONNETERRINA ASPINOSA Tasch, n. sp.
Plate 47, figures 11, 12

Cranidium rectangular in outline; convex, conical glabella shows posterior glabellar furrows curving inward and downward; occipital ring narrow; occipital furrow shallow, defined in equal depth along base of glabella. Free cheeks ending in long, slender genal spines.

Posterolateral limbs not preserved. Occipital ring preserved only in part.

Pygidium unknown.

Relationships.—In lateral profile *aspinosa* bears closest resemblance to *B. prima* Lochman with the exception of the occipital area. The description of *prima* "frontal limb (brim) of medium width; the wide, flat border sharply upturned; anterior margin smoothly rounded" holds for *aspinosa* as well. The two species differ mainly in occipital ring characters. *B. aspinosa* has a narrow occipital ring and lacks an occipital spine while *prima* has a wide occipital ring and large occipital spine.

Remarks.—The species is based on a single cranidium and an associated free cheek. It occurs together with an unde-

termined *Hyolithes* species in black oolitic limestone.

Occurrence.—Loc. 24-f.

Types.—Holotype cranidium, USNM 115643, loc. 24-f.

Genus COOSELLA Lochman 1936

Supplementary description.—Brim varies from concave to varying degrees of convexity.

COOSELLA CONVEXA Tasch, n. sp.
Plate 47, figures 13–15

In addition to the generic characters, cranidia belonging to *C. convexa* show the following curvature in lateral profile view: from the highpoint of convexity of the glabella to a shallow furrow (anterior dorsal furrow), thence downslope as a convex curve (brim) at an angle varying between 30–40 degrees which terminates in a shallow furrow (transverse or marginal furrow), then an outward thrust, low-angled rise (marginal border).

In dorsal view, a narrow, raised ocular ridge proceeds from the outer side of the dorsal furrow in an oblique line. The ocular ridge merges with an outwardly downcurved palpebral lobe, crescentic in outline, which is flat and margins the convex fixed cheek. It appears as if the fixed cheek and its flat, palpebral flap were superimposed on the cranidium. Anterior border thick, rounded, and bearing narrow, transverse furrow and ridge striations.

Pygidium semicircular in outline and has characteristic bilobed appearance (dorsal view) due to incurving of posterior margin at median axial line. The axial lobe is greater than three-fourths the pygidium in length and less than the width of the pleural lobes. Axis and pleura show at least two clearly defined furrows. Pleural furrows end in flat margin which fringes entire pygidium. Pleural furrows slightly elevated above margin in the direction of the upper part of the axis. Side curvature as follows: round posterior of axial lobe tapers downslope in brief straight line which changes direction and proceeds outward to margin. This curvature may be interpreted as a concave curve with slight sag above center.

Relationships.—*C. convexa* is distinguished from all other described species, with the exception of *C. granulosa* Rasetti, by the convex curvature of the brim, the axial lobe length, and the greater width of the pleural lobes of the pygidium. *C. granulosa* has an unfurrowed glabella although "three pairs of smooth areas at the sides of the glabella mark the position of the obsolete glabellar furrows." Its distinguishing characteristic from other *Coosella* species, excluding *convexa*, was described as "the coarser surface ornamentation." While numbers of *convexa* individuals are granulose, others, distinguished in no other way, are not. *C. convexa* specimens, with rare exceptions, have the posterior glabellar furrow clearly defined and the anterior furrows are somewhat fainter. It is possible that *granulosa*, found in a Grosses Roches boulder in western Gaspé, represents a geographic race stemming from the original *convexa* stock. This seems indicated by the absence of glabellar furrows in *granulosa* which otherwise agrees in all essential characters with *convexa*.

Remarks.—Next to *Kingstonia apion*, *C. convexa* is represented by the largest number of specimens, having wide vertical and horizontal range within the formation. The greatest apparent variation between individuals of this abundant species is in the convexity of the brim although many individuals show nearly identical convexity. Certain of the measured constants may be added to the specific description. Thus, in no instance, was the length of the glabella, measured from anterior dorsal furrow to occipital furrow, less than the width of the glabella at its base. In a few instances they were of equal length but in most cases, furrow to furrow, glabella length exceeded width of glabella at its base by less than 1 mm. The absence of surface ornamentation in numbers of *convexa* individuals may possibly be attributed to a combination of circumstances: exfoliation and poor preservation.

Occurrence.—Loc. 24-e, 24-f, 24-d, 24-b, 24-c, 24-h, 24-g.

Types.—Syntype, cranidium and pygidium, USNM 115619, loc. 24-e; pygidium, USNM 115620, loc. 24-b; cranidium, USNM 115621, loc. 24-f.

COOSELLA CONVEXA MAGNALIMBATA
Tasch, n. var.
Plate 47, figures 8, 9

Cranidium square in outline with long, subconical glabella of gentle convexity; glabellar furrows suggested by faint indentations on glabella; occipital ring of medium width; occipital furrow shallow, well-defined only along base of glabella to just within farthest extremities of base. Beyond that, the occipital ring merges with posterior portion of the glabella. Fixed cheeks three-fifths the width of the glabella; palpebral lobe not preserved; ocular ridge crosses fixed cheek diagonally from point below anterior of glabella; dorsal furrow shallow, defines glabella on three sides. Brim granulose, in lateral profile, convex, proceeds at steep angle to very narrow marginal furrow from which there continues, after a slight rise, a flat-lying narrow border, striated anteriorly.

Pygidium and free cheeks unknown.

Relationships.—This variety is readily distinguished from specimens of *C. convexa* proper by its comparatively broad brim and narrow, flat border.

Associated with it in the same bed were *C. convexa* cranidia and pygidia and *Coosella* sp. 2 pygidia.

Remarks.—A single fairly well preserved cranidium showing the distinctive features which are varietal and not specific, is the basis for establishing this new variety.

Occurrence.—Loc. 12.45.

Types.—Holotype, USNM 115622, loc. 12.45.

COOSELLA aff. CONVEXA Tasch
Plate 46, figures 13, 14

Remarks.—A number of cranidia showing closest affinity to *C. convexa* were found together with specimens of that species. However, they differ from *convexa* in the following features: the greater width of the brim, marginal furrow, and in some specimens, the border.

Occurrence.—Loc. 13.3.

Figured specimen.—Cranidium, USNM 115614, loc. 13.3.

COOSELLA VULGARIS Tasch, n. sp.
Plate 45, figures 19, 20

Small cranidium with subquadrate glabella; posterior glabellar furrow deeply indented, anterior furrows faintly marked on some specimens and not visible on others; the most posterior furrows directed inward and downward. Occipital ring of medium width, occipital furrow well defined only at sides; dorsal furrow well defined. Fixed cheeks convex, about one-half the width of the glabella. Palpebral lobe situated on transverse median line of the cranidium. Palpebral furrow shallow, narrow; ocular ridge proceeding from outer side of dorsal furrow, raised above fixed cheek which it crosses diagonally; brim convex, narrow, about same width as frontal border, rises as convex curve between dorsal furrow at anterior of glabella and marginal furrow which separates it from the border that curves and rises above the brim; brim and border together measure slightly less in width than anterior glabellar lobes. Posterolateral limbs short; intramarginal furrow deep, sets off lower narrow convex portion from swollen upper portion of the limb, widens towards extremities.

Facial suture as in genotype. The thorax and the pygidium of this species are as yet unknown.

Relationships.—*C. vulgaris* differs from *convexa* in the narrowness and curvature of the brim; in its fixed cheeks and flat palpebral flap not giving the marked appearance of superimposition on the cranidium as is the case with *convexa;* in its more deeply indented furrows. The average ratio between length of glabella, measured from anterior dorsal furrow to occipital furrow, and width of glabella at its base, is 1.093 for *vulgaris* and 1.127 for *convexa.*

Remarks.—*C. vulgaris,* as the name implies, is a very common species in the present collection and numbers of specimens were available for study. It is of interest that both *convexa* and *vulgaris* occur in several of the same localities.

Occurrence.—Loc. 24-b, 24-d, 24-h, 62-b; Friend's Cove, one-half mile southeast of Hartley, Pennsylvania; Schneider's farm, $3\frac{1}{2}$–4 miles south of Baker Summit.

Types.—Holotype cranidium, USNM 115616, loc. 24-h; paratype cranidium, USNM 115617, loc. 24-b.

COOSELLA sp. undet. 1
Plate 45, figure 14

Cranidium with broadly conical large glabella of gentle convexity, as high as wide, three pairs of glabellar furrows; dorsal furrow shallow, defines glabella on three sides; occipital ring strong; occipital furrow deeply indented on sides, defining swollen posterior glabellar lobes, shallow and arched upward near middle, fixed cheeks convex, less than one-half the width of the glabella; palpebral lobes not preserved; in lateral profile view, brim gently curved downward, ending in shallow, narrow, marginal furrow; border curves up from furrow and forward, standing slightly above brim. Posterolateral limbs elongate, two-thirds width of base of glabella, convex with intramarginal furrow posteriorly.

Exterior of test granulose.

Remarks.—Three cranidia poorly preserved, collected from two nearby localities are assigned here. The nature of the preservation does not allow specific designation. The wider posterolateral limbs, greater width of fixed cheeks, curvature of brim, appear to distinguish this group from other described *Coosella* species.

Occurrence.—Loc. 24-b, 25-g.

Figured specimen.—Cranidium, USNM 115618, loc. 24-b.

COOSELLA sp. undet. 2
Plate 46, figures 19, 20

Pygidium wider than long, with heavy axis narrower than pleural lobes, about one-half length of the pygidium, bearing three segments and a terminal portion the width of two segments; two or more pleural segments; axis high, tapers posteriorly and merges with wide marginal border; border pronouncedly bilobed in appearance. Axis merges with margin by a node-like extension of the terminal portion. Dorsal furrow shallow.

Remarks.—Numbers of pygidia of this species occur in the collection together with cranidia and pygidia of *Blountia prolifica*. In the absence of associated cranidia, the species, which differs from all described *Coosella* species, is tentatively left undetermined.

Occurrence.—Loc. 13.3, 25-g, 24-b, 107-k.

Figured specimen.—Pygidium, USNM 115615, loc. 13.3.

Genus COOSIA Walcott
COOSIA ? PUSTULATA Tasch, n. sp.
Plate 47, figure 10

Cranidium subquadrilateral in outline with a large, broadly conical glabella of gentle convexity; narrow median longitudinal ridge on glabella, on either side of which glabellar furrows are faintly defined anteriorly; dorsal furrow deep, broad, defines glabella on three sides; posterior lateral limbs unknown. Fixed cheeks equal to, or slightly greater than, one-half the width of the glabella; same slight convexity as glabella; ocular ridge narrow, raised, diagonal across fixed cheek. In lateral profile view, brim of medium width, proceeding from anterior dorsal furrow briefly thrust upward and forward, proceeds with gentle convexity and enters broad, shallow marginal furrow; marginal furrow bounded anteriorly by a steeply rising, narrow border. Border attains the approximate height of the highest point on the convex brim.

Fixed cheeks and brim covered with numerous pustules.

Associated pygidium tentatively assigned to *pustulata*, wider than long; smooth; axial lobe raised, less than two-thirds the length of the pygidium, narrow; two axial segments and terminal portion which merges with border by node-like extension; two pleural segments clearly defined. Pleural lobes convex, about equal to axis in width; marginal border wide, slightly concave where node-like extension of axial lobe joins it; under surface of border exposed showing delicate horizontal depressions appearing like scratch lines. Shallow dorsal furrow defines tapering axis. Some pygidia show shallow marginal furrow. Bilobed appearance of marginal border absent.

Relationships.—Lochman (1936, pp. 35–43) observed of the genus *Coosella* that it "is closely related to *Coosia* but differs from it in two features, namely, the presence of a transverse furrow (marginal furrow) on the cranidium, and in the pronounced bilobed appearance of the marginal border." However, Walcott, in establishing the genus

Coosia (1912b, p. 94), observed that the brim "slopes gently downward to a shallow furrow that serves to distinguish it from the frontal border." In light of the presence of the "shallow furrow" described by Walcott, and the absence of a bilobed appearance to the marginal border of the pygidium that Lochman ascribes to *Coosella*, the species is here tentatively assigned to *Coosia*.

Coosia ? pustulata differs from all other described *Coosia* species chiefly in the narrowness of its border compared to the brim, the occurrence of pustules on fixed cheeks and brim, the width of its fixed cheeks.

Remarks.—Associated with this species were cranidia of *Coosella convexa*, cranidia and pygidia of *Blountia prolifica*, *Tricrepicephalus arcuatus*, and specimens of *Coosella* sp. 2, and *Coosella* aff. *convexa*.

Occurrence.—Sparsely represented in the collection. Loc. 13.3.

Types.—Holotype cranidium, USNM 115645, loc. 13.3.

Genus CREPICEPHALUS Owen 1852

CREPICEPHALUS sp. undet. 1

Plate 46, figure 12

The gentle convex curvature of the flat, marginal border terminates at the posterolateral corners in brief, blunt points which are the roots of pygidial spines. The pointlike terminus is not to be confused with pygidial spines of the type of *C. brevispinus;* rather, it is the type of *C. snowyensis.*

Remarks.—Only a partially preserved pygidium and its mold were collected by the writer at one horizon.

Occurrence.—Rare in the present collection. Loc. 13.2.

Figured specimen.—Pygidium, USNM 115646, loc. 13.2.

Genus GENEVIEVELLA Lochman 1936

Remarks.—Walcott (1913, p. 170) defined *Chuangia* as a genus characterized by "a narrow, concave frontal limb" among other features. He noted that "in *Chuangia* the frontal limb and rim meet to form an angle and the rim does not rise above the upward sloping surface of the frontal limb." The nature of the frontal limb (brim) in *Genevievella*, an important generic character, sets it apart from *Chuangia* and raises doubts as to the suggested close relationship between the two genera.

GENEVIEVELLA CAMPBELLINA

Tasch, n. sp.

Plate 46, figures 17, 18; plate 47, figure 1

Cranidium small, with subquadrate glabella of gentle convexity, curvature decreases in shorter space and to greater extent anteriorly than posteriorly, anterior end of glabella variable in elevation above marginal furrow. Occipital furrow deep and narrow; dorsal furrows well defined, merge anteriorly with straight, shallow and broad marginal furrow. Fixed cheeks of variable convexity; palpebral lobes not preserved; ocular ridge prominent, proceeding diagonally across fixed cheek from dorsal furrow just below anterior end of glabella. Brim curved towards marginal furrow, terminated abruptly by that furrow anteriorly and by the raised ocular ridge posteriorly. Frontal border narrow, gently curved forward giving an appearance of being almost flat; anteriormost portion shows raised horizontal striations, periphery gently and uniformly curved. Posterolateral limbs moderately elongate, extremities not preserved; intramarginal furrows terminate below posterior end of dorsal furrow and slightly below occipital furrow. Course of facial suture imperfectly preserved.

Thorax unknown.

The border of an associated free cheek is as wide as that found on the cranidium and bears horizontal ridges on the anterior portion; it appears to taper to a genal spine. A furrow resembling the marginal furrow of the cranidium runs along the entire inner border and from it rises a gently curved ocular platform.

The associated pygidium is semicircular in outline; axial lobe about three-fourths the length of pygidium, consisting of five segments and a small terminal portion, tapers posteriorly; widest portion wider than pleural segments, elevated above these segments. Outline of pleural lobes forms wide "V", each arm of which is on either side of the axial lobe. Pleural lobes have four segments that leave the elevated "V"

area and continue along concave course almost to the narrow flat margin. Pleural segments straighten out in downward direction as they leave elevated area. Axial and pleural segments bear small, raised, pustule-like mounds that are scattered over the surface.

Relationships.—This species derives its name from *G. campbelli* Resser with which it shares in common the character of a straight marginal furrow. However, it differs from that species in the character of its border and in its subquadrate glabella. The frontal border of *campbellina* is uniformly narrow and arcuate, whereas in *campbelli* it is wider along the midpart, and arched. The pygidium of *campbellina* has closest affinities to *G. etelka*.

Remarks.—*G. campbellina* is based on several cranidia and tentatively assigned to it are an associated free cheek and pygidium found in a separate piece of rock of the same lithology at the same locality (24-d) where some of the *campbellina* cranidia were collected.

Occurrence.—Loc. 24-d, 24-f, 107-k; 11.12, 12.57.

Types.—Holotype cranidium and pygidium, USNM 115638, loc. 107-k, 24-d; paratype, USNM 115639, loc. 24-d, paratype cranidium, USNM 115640, 107-k.

GENEVIEVELLA (?) PENNSTATENSIS
Tasch, n. sp.
Plate 44, figure 7

Cranidium small, wider than long, with prominent subquadrate convex glabella rounded in front; no glabellar furrows; occipital furrow shallow and narrow, very faint; occipital ring narrow; dorsal furrow completely defines glabella. Fixed cheeks convex, less than one-half width of glabella; palpebral lobes situated near upper third of glabella; no definable brim; fixed cheeks separated from frontal border by elevation anterior to palpebral lobe upon which faint ocular ridge proceeds diagonally towards a point on the anterior outer side of the dorsal furrow; anterior dorsal furrow separates glabella from the border; border downsloping, short, terminating in horizontal striae. Posterolateral limbs same width as base of glabella, marked by intramarginal furrow of same faintness and shallowness as occipital furrow. Free cheeks unknown.

Thorax and pygidium unknown.

Remarks.—This species is based on three small, well preserved cranidia. The writer considers the lack of a definable brim as one of the critical diagnostic characters of *Genevievella*. Thus, even though the individuals assigned to *pennstatensis* lack a shallow marginal furrow as such, separation of fixed cheeks and glabella from the narrow frontal border is achieved, as shown in the above description. Accordingly, this species is tentatively assigned to *Genevievella*.

Occurrence.—Loc. 24-d, 12.66.

Types.—Holotype cranidium, USNM 115641, loc. 24-d.

GENEVIEVELLA PLESIOCHIELUS
Tasch, n. sp.
Plate 46, figures 15, 16; plate 44, figure 5

Cranidium with convex glabella; glabellar furrows faint; convex fixed cheeks of holotype, 1.5 mm., glabella 3.8 mm. in width, that is, the former is less than one-half the width of the glabella. Brim convex, represented by area in front of ocular ridge which runs diagonally from dorsal furrow across fixed cheek. Greatest width of brim between ocular ridge and marginal furrow in holotype cranidium is 1.5 mm. Downsloping front of glabella protrudes onto border beyond anterior of brim.

Border flat, terminating in a short, thick, vertical band that slopes below the gently arched periphery of the border. The end portions of the brim are bent downward. Posterolateral limbs of holotype 4.9 mm. long, greatest width 2.0 mm., marked by narrow, intramarginal furrow which begins at dorsal furrow, curves around the inner portion of the posterior limb, and proceeds diagonally downward.

Pygidium relatively large, axial lobe convex, reaches near to posterior margin, same width as pleural lobes; pleural lobes slope away from axial lobe abruptly reaching narrow, flat marginal border. Axial segments not preserved; four segments on pleural lobe.

Minute granules cover occipital ring of cranidium.

Relationships.—*G. plesiochielus* has closest

affinities to *G. tumida* but differs from it as follows: *plesiochielus* has a flat border, fixed cheeks less than one-half the width of the glabella, intramarginal furrow that does not broaden; *tumida* has a convex border, fixed cheeks one-half the width of the glabella, intramarginal furrow that broadens.

Remarks.—The main cranidial character which distinguishes *plesiochielus* from all other described *Genevievella* species is given by the following measurements of the holotype: width of border along median line of glabella where it contacts anterior of glabella, 0.9 mm.; width where it contacts anterior of brim, 1.1 mm. Thus, front of glabella protrudes about 0.2 mm.

Occurrence.—Rare in present collection. Loc. 24-e.

Types.—Holotype cranidium, USNM 115637, loc. 24-e.

Genus HALLASPIS Raasch and Lochman 1943

HALLASPIS MATUTINA (Hall)

Plate 44, figures 11, 12

Amphion ? matutina HALL, 1863, New York State Cabinet of Natural History, 16th Ann. Rpt., p. 222, pl. 5a, fig. 6; 1867, Trans. Albany Inst., vol. 5, p. 194.

Amphion ? matutina WALCOTT, 1916, Smithsonian Misc. Coll., vol. 64, no. 3, p. 219, pl. 26, fig. 8.

Acheilus matutina RAYMOND, 1924, Vermont State Geol. Report, p. 167.

Stenochilina matutina RESSER, 1936, Smithsonian Misc. Coll., vol. 95, no. 4, p. 27.

Hallaspis matutina (Hall), RAASCH & LOCHMAN 1943, Jour. Paleontology, vol. 17, no. 3, pp. 230–231, pl. 34, figs. 14–17.

Original description.—Glabella gibbous, longer than wide, sub-ovate, rounded, and a little wider in front. Occipital ring narrow and straight, occipital furrow narrow. Posterior lobe a little oblique, the furrow deeply impressed and a little expanded at its inner extremity; median lobe with the sides nearly parallel, separated from the anterior lobe by a narrow, distinct furrow; anterior lobe broad, the length somewhat less than half the entire length of the glabella, a scarcely defined depression extending obliquely from near the middle of its length to the front.

Additional description.—Hall's "scarcely defined depression" is actually a brim thinning out from either side of the anterior portion of the glabella to the medial region where it appears as a narrow depression. The entire brim terminates in a vertical border which, after its brief rise above the brim, curves forward. At either end the border gently curves around the anterior portion of the fixed cheek, the inner side of which merges with the posterior portion of the widest area of the brim.

Some specimens show a posterior furrow (dorsal view) in occipital ring on either side of root of short, stout spine, others do not.

Test granulose.

Occurrence.—Sparse in present collection. Loc. 24-b.

Types.—Plesiotype, USNM 115628, loc. 24-b.

Genus HOLCACEPHALUS Resser

HOLCACEPHALUS TUNDA ATYPICALA Tasch, n. var.

Plate 44, figures 25, 26

Cranidium similar to *H. tunda* though different from it in several features which seem to be more varietal than specific in nature. *H. tunda* has no glabellar furrows while *tunda atypicala* shows this generic character; the posterior glabellar furrows curve inward and downward defining small, swollen posterior lobes on the sides of the glabella; other furrows faint. Fixed cheeks slightly wider than glabella, not as great as one and one-half times the glabella as in *tunda*. In lateral profile the convex brim and border are more gently sigmoid in shape than in *tunda* and the brim departs from the vertical in the direction of the marginal furrow much more than in *tunda*. In front dorsal view, this feature is seen in the less inflated brim.

Remarks.—A single cranidium found in black oolitic limestone is the only representative of *Holcacephalus* in the present collection. This specimen, however, is excellently preserved.

Occurrence.—Loc. 24-d.

Types.—Holotype cranidium, USNM 115636, loc. 24-d.

Genus ITHYCEPHALUS Resser 1938

Original description.—Small simple trilobite. Cranidium semicircular in outline. Glabella rectangular, highly arched longitudinally, occupying the full length of the cranidium except for a narrow, concave simple brim. Occipital furrow clearly defined, glabellar furrows lacking. Fixagenes without posterior furrows, roughly triangular in shape, averaging about two-thirds as wide as the glabella. Eyes small, situated forward of the center of the cranidium.

ITHYCEPHALUS sp. undet.
Plate 44, figure 21

Remarks.—The three minute cranidia assigned to this genus show the main generic characters, namely, the rectangular glabella occupying the full length of the cranidium; the narrow simple brim. However, they differ from the genotype, *I. typicalis* in having fixed cheeks which are wider than the glabella along the median line of the cranidium, and in having an intramarginal furrow. The material available is insufficient to determine whether these variations are of minor or of specific value.

Occurrence.—Loc. 24-f, 12.61.

Figured specimen.—Cranidium, USNM 115642, loc. 24-f.

Genus KINGSTONIA Walcott 1924
KINGSTONIA APION Walcott
Plate 44, figures 23, 24, 27, 28

Kingstonia apion WALCOTT, 1924, Smithsonian Misc. Coll., vol. 75, no. 2, p. 58; 1925, Smithsonian Misc. Coll., vol. 75, no. 2, p. 103, pl. 16, figs. 27–28a.

Kingstonia apion Walcott, RESSER, 1938, Geol. Soc. America Special Paper 15, p. 82, pl. 12, figs. 1–2.

Supplementary description.—Border: In *apion* the thin border may be confined to the anterior portion of the area defined by the dorsal furrows laterally bordering the glabella. In that event the suture extending forward from the eyes and cutting the border abruptly will cut it close to where the dorsal furrow, if extended anteriorly, would cut it. Or the border may extend slightly beyond the dorsal furrow limits. In that event, when cut by the suture extending forward from the eyes, a wider anterior area of the fixed cheek is defined.

Limbs: Posterolateral limbs of the cranidium vary from shapes that approximate an isosceles triangle where one side is the dorsal furrow, to a right triangle. The former is the "elongate" type of limb. Other terms in use are "long" or "prominent" limb. The latter is the "short" type of limb. The holotype of *apion* had "elongate" limbs and a border extending slightly beyond the dorsal furrow limits.

Pygidium: Under proper lighting, five external segments are visible on the axis. Exfoliated specimens show up to four clearly defined internal segments on the pleural lobes. The axis extends for three-fourths of the length of the pygidium, tapering slightly posteriorly and terminating by merging in a steeply descending thick edge. The axis is on the average about one-third the width of the pygidium.

Occurrence.—The most abundant species in the Warrior, having a wide horizontal and vertical range within the formation. Loc. 24-f, 24-d, 24-g, 24-e, 24-b, 7341.

Types.—Plesiotype, USNM 115598, cranidium, 24-f; USNM 115599, pygidium, 24-b.

KINGSTONIA ARA (Walcott)
Plate 45, figures 4, 5

Ucebia ara WALCOTT, 1924, Smithsonian Misc. Coll., vol. 75, no. 2, p. 60, pl. 14, fig. 4; WALCOTT, 1925, Smithsonian Misc. Coll., vol. 75, no. 3, p. 118, pl. 17, figs. 7–8.

Kingstonia ara (Walcott), RESSER, 1936, Smithsonian Misc. Coll., vol. 95, no. 4, p. 24; RESSER, 1943, Smithsonian Misc. Coll., vol. 103, no. 5, p. 51, pl. 8, figs. 42–46.

Kingstonia ara (Walcott), LOCHMAN, 1938, Jour. Paleontology, vol. 12, no. 5, p. 466, pl. 57, figs. 5–8.

Original description.—(Walcott, 1924) "*Ucebia* is closely allied to *Kingstonia* but differs by having a shallow dorsal furrow."

Supplementary description.—(Walcott, 1925) "Lacks frontal limb (brim) as the glabella extends to the frontal rim (border) . . . The suture follows the same course as in *Kingstonia* passing very nearly through the genal angles. The eyes are also small and hold about the same position with respect to the anterior and posterior ends of the suture but not as regards the anterior extremity of the glabella."

Revision of Ucebia *to* Kingstonia.—(Resser, 1936) "*Ucebia* is not a valid genus. When the shell is removed, any species of *Kingstonia* becomes *Ucebia*."

It is curious that there is as yet no diagnostic description of the cranidia of *K. ara* although Walcott's description has been supplemented twice. Accordingly, one is given below to be taken with Lochman's description of the pygidia and Walcott's 1925 supplementary description.

Diagnostic features of K. ara.—Cranidium with glabella of very gentle convexity in vertical direction. This diagnostic curvature corresponds to the absence of a brim

("frontal limb" of Walcott). Dorsal furrows deeply indented, widening posteriorly; convex posterolateral limbs slightly shorter than width along the base of the glabella.

Relationships.—The gentle convexity of *K. ara* in lateral profile, giving it an almost flat appearance, differentiates it from *apion* and *walcotti.*

Occurrence.—Rare in the present collection. Loc. 24-b. (Walcott described the species from material collected at loc. 24-f.)

Types.—Plesiotype, USNM 115603, 24-b.

KINGSTONIA CHEILUSIS Tasch, n. sp.
Plate 45, figure 15

Four characters of the cranidium distinguish this species. Extremely gentle convexity along line drawn vertically through glabella; sudden indentation of the brim a short distance from the border; slight restoration of brim's curvature in opposite or border direction; the facial suture in dorsal view has an almost straight course both where it cuts the border and where it proceeds within the genal angle.

Pygidium and free cheeks unknown.

Relationships.—*K. cheilusis* differs from *apion* in diminished convexity in a vertical direction and in the straightening out of the facial suture. None of the *Kingstonia* species shows an interruption in brim curvature comparable to that in *cheilusis.* It has closest affinities to *trapezoidia* but differs from it in having lesser convexity, in straightness of suture, and in brim curvature described above.

Occurrence.—Few specimens, sparsely distributed. Loc. 24-f, 24-c.

Types.—Holotype, USNM 115597, loc. 24-f.

KINGSTONIA TRAPEZOIDIA Tasch, n. sp.
Plate 44, figures 8–10

Characterized by cranidia (without reference to convexity) which more closely approximate a general trapezoidal form dorsally than any other species. This form is the result of a wider pre-ocular area. The area is defined by a suture behind the small convex palpebral lobe cutting the brim well beyond where the dorsal furrow would cut it, if extended, and by a slightly elevated brim. The brim is relatively wider than in other species. Border with seven parallel striae or transverse ridges which tend to anastomose.

Outer surface punctate.

Relationships.—*K. apion* shows a marked concavity along the sides of the fixed cheeks, particularly in the ocular region. In *K. trapezoidia* this portion tends to straighten out. *K. trapezoidia* has a more pronounced convexity than *apion* with greatest convexity across the posterolateral limbs; *apion* has uniform convexity. Compared to *walcotti, K. trapezoidia* has a gentler convexity

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EXPLANATION OF PLATE 46

FIGS. *1, 2*—*Lonchocephalus planus* Tasch, n. sp. Holotype, dorsal and side views of cranidium, ×3½, USNM 115610, loc. 11.12. (p. 299)

3–5—*Modocia benorensis* Tasch, n. sp. *3, 4*, Holotype, dorsal and side views of cranidium, ×2; *5*, holotype, dorsal view of weathered pygidium, ×2, USNM 115609, loc. 107-k (=7291 Bellefonte Quad.). (p. 301)

6–9—*Blountia waddlensis* Tasch, n. sp. *6, 7*, Holotype, side and dorsal views of cranidium, ×1½; *8, 9*, holotype, dorsal and side views of pygidium, ×1¼, USNM 115604, loc. 25-g. (p. 287)

10, 11—*Pemphigaspis intermedia* Tasch, n. sp. Syntype, dorsal and side views of perfectly preserved half of a pygidium, ×2¾, USNM 115630, loc. Bellefonte Quad. 7294, 7341. (p. 302)

12—*Crepicephalus* sp. undet. 1. Half of a pygidium showing where pygidial spine has been broken off, wide border and three segments of right pleural lobe, ×2¾, USNM 115646, loc 13.2. (p. 292)

13, 14—*Coosella* aff. *convexa* Tasch. Dorsal and side views of cranidium showing characteristic marginal furrow, ×2; USNM 115614, loc. 13.3. (p. 290)

15, 16—*Genevievella plesiochielus* Tasch, n. sp. Holotype, dorsal and side views of cranidium, ×2¼, USNM 115637, loc. 24-e. (p. 293)

17, 18—*Genevievella campbellina* Tasch, n. sp. *18*, Holotype, dorsal view of cranidium, ×3½, USNM 115638, loc. 107-k; *17*, paratype, dorsal view of cranidium, ×3½, USNM 115639, loc. 24-d. (p. 292)

19, 20—*Coosella* sp. undet. 2. Dorsal and side views of pygidium, ×2, USNM 115615, loc. 13.3. (p. 291)

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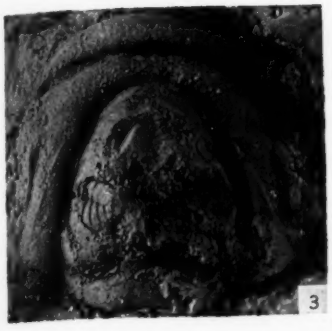
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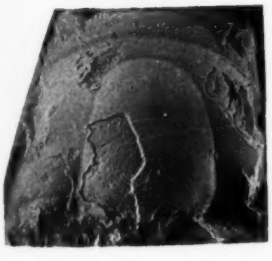
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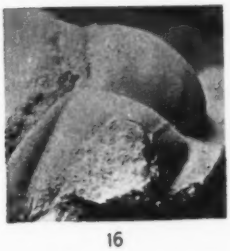
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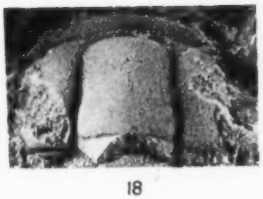
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Tasch, Cambrian Warrior limestone fauna

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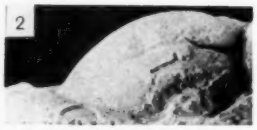
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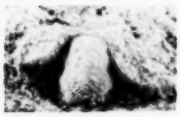
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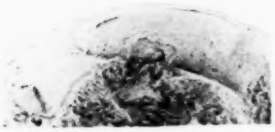
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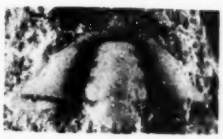
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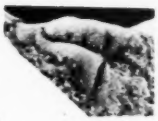
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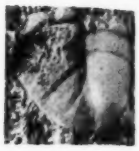
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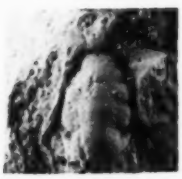
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Tasch, Cambrian Warrior limestone fauna

in the region of the brim. It differs from both *apion* and *walcotti* in that its brim extends farther beyond the palpebral lobe than in either of these species.

Remarks.—The occurrence of *trapezoidia* together with *apion* and/or *walcotti* on the same slab of rock and at several different horizons at which the writer made collections, suggests the possibility of a more intimate relationship between the three species than present knowledge allows one to infer. That is to say, as our knowledge of the kingstonids expands, such progress being largely a function of collecting more and better specimens from numbers of Upper Cambrian horizons, it may be possible to establish that the three species discussed above are varieties of one species rather than distinct species.

Occurrence.—Relatively abundant. Loc. 24-b, 24-f, 24-d; 12.3, 12.66, 12.75, 12.79.

Types.—Holotype, USNM 115601, paratype, USNM 115602, loc. 24-f.

KINGSTONIA ULRICHI Tasch, n. sp.
Plate 44, figures 18–20

In lateral profile, a gentle arc uniformly tapering anteriorly and posteriorly characterizes the curvature of the cranidium. Dorsal furrows faintly define narrow, elevated glabella and terminate as faint arcuate furrows on either side of the anterior of the glabella. Medial anterior sector of glabella merges with brim without change of slope. Brim terminates in usual kingstonid striated border. Fixed cheeks convex, about two-thirds the width of the glabella along medial line, continue downward at an angle of about fifty degrees and outward to form convex, broad posterolateral limbs 2 mm. long in holotype and arcuate on the outer side. The limbs continue well below the base of the glabella.

Facial suture follows straight course and converges slightly in front of eyes, thence forming a gentle concave curve and proceeding downward and outward.

Area of occipital and intramarginal furrow not preserved. Thorax unknown.

Smooth, flat pygidium. Long and short varieties. On the average, short tails from 2–4 mm. long and 3–5 mm. wide; long tails from 4–6 mm. long and from 4.5–6.0 mm. wide. Short tail, semicircular in outline; axis one-third width of pygidium, bounded by sharply defined furrows on either side which tend to converge posteriorly; these dorsal furrows extend for two-thirds to

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EXPLANATION OF PLATE 47

FIGS. *1*—*Genevievella campbellina* Tasch, n. sp. Holotype, dorsal view of pygidium, ×3¼, USNM 115638, loc. 107-k. (p. 292)

2–4—*Blountia prolifica* Tasch, n. sp. *4*, Holotype, dorsal views of cranidium and pygidium, ×¾; *3*, holotype, side view of pygidium, ×2¼; *2*, holotype, side view of cranidium, ×2¼; USNM 115606, loc. 13.3. (p. 286)

5, 6, 21—*Blountia* sp. undet. 1. *5*, *6*, Dorsal and side views of pygidium, ×2¾; *21*, free cheek, ×2¾, USNM 115608, loc. Old Quarry near Waddle. (p. 288)

7—*Menomonia calymenoides* (Whitfield). Plesiotype, dorsal view of cranidium, ×3¾, USNM 115644. loc. 24-d. (p. 300)

8, 9—*Coosella convexa magnalimbata* Tasch, n. var. Holotype, dorsal and side views of cranidium, ×2¼, USNM 115622, loc. 12.45. (p. 290)

10—*Coosia ? pustulata* Tasch, n. sp. Holotype, dorsal view of partially preserved cranidium, ×1½, USNM 115645, loc. 13.3. (p. 291)

11, 12—*Bonneterrina aspinosa* Tasch, n. sp. Holotype, dorsal and side views of cranidium, ×2¾, USNM 115643, loc. 24-f. (p. 288)

13–15—*Coosella convexa* Tasch, n. sp. *13*, Syntype, dorsal view of cranidium together with dorsal oblique view of pygidium, ×2¼, USNM 115619, loc. 24-e; *14*, syntype, dorsal view of pygidium, ×3½, USNM 115620, loc. 24-b; *15*, syntype, dorsal view of cranidium, ×3, USNM 115621, loc. 24-f. (p. 289)

16–20—*Llanoaspidella warriorsmarkensis* Tasch, n. gen., n. sp. *19, 20*, Holotype, dorsal and side views of cranidium showing absence of occipital furrow except on posterior sides of glabella, ×2¾, USNM 115631, loc. 24-f; *17*, paratype, dorsal view of cranidium showing nature of connectives between occipital ring and glabella, ×2¾, USNM 115632, loc. 24-g; *18*, paratype, dorsal view of partly preserved cranidium bearing faint ocular ridge, ×3½, USNM 115633, loc. 24-g; *16*, paratype, dorsal view of cranidium showing blunt border wedge to which marginal furrows form two equal arcuate sides, ×2¾, USNM 115634, loc. 24-b. (p. 299)

three-quarters the length of the pygidium and where they terminate the curvature continues unchanged and then abruptly terminates in a narrow vertical band. A similar band, somewhat narrower, margins the pleural segments. Long tail variety semicircular to subtriangular and suboblong.

For both varieties, axis rises slightly above pleural lobes; no furrows or segments visible on outer surface.

Relationships.—A long tail exfoliated specimen shows no pleural or axial furrows. The *ulrichi* pygidia differ from those of *Bynumia* in the following aspects: the pleural lobe is not wider than the axial, the absence of transverse ridges on the narrow vertical band, the sharp definition of dorsal furrows, the occurrence of long and short tail varieties. They resemble *Bynumia* most closely in smoothness, flatness, and the occurrence of a narrow, vertical band. The cranidium of *ulrichi* differs from all other described kingstonid cranidia in the more elongate downcurved posterolateral limbs. It apparently has closest affinities to *K. gaspensis* Rasetti. However, it lacks definition of glabella anteriorly, has a differentiated border, and posterolateral limbs of greater downward extension. The long and short varieties of pygidia likewise differ from *gaspensis* in the presence of well-defined furrows paralleling the axis on the outer surface and a narrow vertical band.

Name.—Although this species is based, in part, on material collected by the writer, it is named for Dr. E. O. Ulrich who, working only with pygidia, clearly recognized that long and short varieties belonged to the same "new" species.

Occurrence.—Both long and short pygidia relatively numerous at several localities. Occurrences of heads and tails together are rare. Long tail, 24-d, 24-b; short tail, 24-d, 24-f; head and tail together, 12.79.

Types.—Syntype, cranidium and pygidium, USNM 115596, loc. 12.79; long pygidium, USNM 115595a, loc. 24-d; short pygidium, USNM 115595b, loc. 24-d.

KINGSTONIA WALCOTTI Resser
Plate 44, figures 6, 16, 17

Kingstonia walcotti RESSER, 1938, Geol. Soc. America Special Paper 15, p. 83, pl. 12, figs. 3–4.

Kingstonia walcotti Resser. LOCHMAN, 1940, Jour. Paleontology, vol. 14, no. 1, p. 35, pl. 4, figs. 13–16.

Kingstonia walcotti Resser. LOCHMAN & DUNCAN, 1944, Geol. Soc. America Special Paper 54, p. 113, pl. 14, figs. 21–26.

Original description.—(Resser) "This species is characterized by its width and the bluntness of the triangular posterolateral limbs."

Remarks.—*K. walcotti* may turn out to be a variety of *apion* rather than a separate species (see p. 297).

Occurrence.—*K. walcotti* pygidia are more numerous than cranidia in this collection and while the number of individuals is large, it is less than the number of individuals of *apion*. Loc. 25-i, 24-f, 24-b; 12.82, 12.79, 11.12.

Types.—Plesiotype, USNM 115600, loc. 24-f.

Family LLANOASPIDAE Lochman 1944

Remarks.—Description of pygidium is excluded since none are described below. It will be noted that the diagnostic features of the family are the "marked tendency towards obsolescence on median line" shown by transverse (marginal) furrow and the "curving forward" of the intramarginal furrow.

Genus LLANOASPIDELLA Tasch, n. gen.

Cranidium subtrapezoidal in outline; glabella blunt-topped, conical, convex; three pairs of short glabellar furrows, posterior two of these are arcuate. Dorsal furrows deep, set glabella off in strong relief, merge posteriorly with very narrow, straight furrow which serves as a boundary between the blunt wedge formed by the posterior median portion of the border and the wider blunt top of the anterior glabellar lobe. Marginal furrow split into two arcs which form equal arcuate sides of the blunt border wedge described above. Border slightly curved forward; ends in slightly striated rim. Posteriorly, dorsal furrows merge with occipital furrow which is tangent to swollen portion of posterior glabellar lobe on either side and discontinuous or continuous across base of glabella. Occipital ring merged with base of glabella by sheath-like continuation, ring roughly triangular in shape; from its

anterior portion, two narrow connectives attach to inner posterior side of dorsal furrows.

Posterolateral limbs together with fixed cheeks (both convex), with dorsal furrow acting as one side, and intramarginal furrow as another side, approximate an equilateral triangle in form. Intramarginal furrow does not change its slightly arcuate course towards margin.

Ocular ridge arcuate, proceeds from outer side of dorsal furrow across fixed cheek.

Facial suture cuts anterior margin out at side, proceeds inward to marginal furrow and outward to palpebral lobe. Course in region of palpebral lobe unclear. Beyond that it continues parallel to dorsal furrow to about lower third of glabella and then continues outward to within the genal angle.

Remarks.—The subtrapezoidal shape of the cranidium, the uninterrupted, slightly arcuate course of the intramarginal furrow, the nonelongate glabella, and the sheath-like and thin side connectives that link the occipital ring to the glabella, distinguish this genus from *Llanoaspis*.

Genotype.—*Llanoaspidella warriorsmarkensis* Tasch, n. gen., n. sp.

LLANOASPIDELLA WARRIORSMARKENSIS Tasch, n. sp.
Plate 47, figures 16–20

In addition to the characters necessarily given in the generic description, the border is about two-fifths the length of the base of the cranidium along a line drawn through the genal angles; border ends in faintly striated brim.

Occurrence.—Relatively numerous in present collection. Lower part of Warriorsmark section, and 1 mile southeast of Waddle.

Types.—Holotype, USNM 115631, loc. 24-f; paratype, USNM 115632, loc. 24-g; paratype, USNM 115633, loc. 24-g; paratype, USNM 115634, loc. 24-b.

LLANOASPIDELLA BIGENUSIA Tasch, n. sp.
Plate 44, figures 14, 15

This species has the continuous occipital furrow of *Llanoaspis* and the side connectives parallel to the furrow where it is tangent to the swollen portion of the posterior lobe of the glabella. Occipital ring triangular, has its apex produced farther back from occipital furrow and terminates in a spine.

Relationships.—*L. bigenusia* differs from *warriorsmarkensis* by the dual occurrence of a continuous occipital furrow and connectives to base of the glabella from anterior sides of occipital ring.

Occurrence.—Sparse in present collection. Loc. 7285, Bellefonte Quadrangle; second roadcut along Highway Number 322, south of Waddle Road, Pennsylvania.

Types.—Holotype, USNM 115635, loc. 7285.

Genus LONCHOCEPHALUS Owen 1852

LONCHOCEPHALUS PLANUS Tasch, n. sp.
Plate 46, figures 1, 2

Cranidium subquadrate with broadly conical, large, convex glabella, slightly longer than wide; two pairs of faint glabellar furrows; dorsal furrow narrow, defines glabella on three sides; occipital furrow convex towards center, more sharply defined than dorsal furrow; occipital ring triangular in shape with apex merging into base of short, tapered spine. Posterolateral limbs two-thirds width of base of glabella, with broad, deep, intramarginal furrow. Fixed cheeks convex, about one-half width of glabella; palpebral lobes unknown; low, narrow ocular ridge proceeds from point slightly posterior to top of glabella on outer side of dorsal furrow diagonally across fixed cheek; brim same width as border, straight anterior to glabella but convex above ocular ridge, separated from arcuate border by shallow, faint marginal furrow.

Free cheeks granulose on outer surface, small, longer than wide; ocular platform convex; marginal furrow narrow, shallow; marginal border narrow, flat; small, pointed anterior projection and a short, stout spine directed outward.

Facial suture cutting anterior margin far out at sides, directed inward to marginal furrow and outward, apparently curving around palpebral lobes; thence curving with slight concavity outward and backward. Further course of suture unknown.

Pygidium unknown. Outer surface of test smooth.

Relationships.—The most distinctive specific character of *planus* is the flatness of its brim. This contrasts with the convex brims

of the lonchocephalids described by Walcott and others.

Remarks.—Several cranidia in the present collection. Loc. 24-d, 24-f, 11.12, 12.9.

Types.—Holotype cranidium, USNM 115610, loc. 11.12.

LONCHOCEPHALUS SWARTZI Tasch, n. sp.
Plate 45, figures 16, 17

Cranidium ovate with convex, large, subquadrate glabella; two pairs of glabellar furrows, posterior pair directed inward and downward. Occipital furrow narrow, deeply indented along swollen posterior lobes of glabella; occipital ring narrow, flat, extending into a slender, slightly upturned spine; posterolateral limb not preserved. Fixed cheeks convex, one-half width of glabella. Ocular ridge slightly raised, very narrow, extending across fixed cheeks diagonally; dorsal furrow shallow; brim short, steeply convex, merges with shallow, narrow marginal furrow; border narrow, briefly thrust forward from furrow and curved downward; terminates in series of line-like horizontal ridges.

Thorax unknown.

Pygidium semicircular; axis high, segmentation concealed; pleural lobes convex, five furrows visible in exposed portion, ends in a narrow, flat, continuous border on which terminal node of axis projects, and to which axial node is joined by a slightly concave connection.

Relationships.—The steep convexity of the short brim is the chief specific character differentiating *swartzi* from other described species. In addition, other characters distinguish *swartzi* from certain species. For example, *montanensis* has flat, fixed cheeks whereas *swartzi* has convex fixed cheeks.

Name.—The species is named for Dr. F. M. Swartz who found the described specimens.

Remarks.—Two cranidia and a partly concealed pygidium are the material upon which this distinctive species is based.

Occurrence.—Lower exposed Warrior beds, Friend's Cove, half a mile northeast of Hartley in southwestern part of Everett Quadrangle.

Types.—Holotype cranidium and partly concealed pygidium, USNM 115611, loc. Friend's Cove.

LONCHOCEPHALUS WADDLEI Tasch, n. sp.
Plate 45, figures 1–3

Cranidium rectangular, of gentle convexity; large, subquadrate glabella; two pairs of glabellar furrows, posterior furrows arcuate; dorsal furrows narrow, shallow; occipital furrow continuous, follows deeply indented, concave course around swollen posterior portion of glabellar lobe and proceeds across median region parallel to base of glabella as a shallow indentation; occipital ring joined anteriorly by narrow connectives issuing from its sides to inner side of dorsal furrow, posteriorly converges to form thick based, tapering spine slightly curved beyond root area. Posterolateral limbs unknown. Fixed cheeks convex, about one-third width of glabella. Ocular ridge faint, runs from outer side of dorsal furrows in downsloping arc across anterior portion of fixed cheek.

Brim about as wide as the distance between glabellar furrows measured on side of glabella; in lateral profile view, proceeds from anterior of glabella gently downslope, then completes short, convex curve that is greater in some specimens than in others, and continues downslope (marginal furrow), and beyond furrow rises to form a forward thrust, rounded border which is elevated above the height of the brim. Appearance in dorsal view: a curved, ring-like brim around which a thicker, ring-like, more gently curved border appears; the two "rings" separated by a deeply indented marginal furrow.

Course of facial suture obscured. Test granulose.

Remarks.—*L. waddlei* differs from other described species in having a ring-like brim and border and in the gentle convexity of its glabella.

Occurrence.—Sparse in present collection. Loc. 24-b.

Types.—Holotype cranidium, USNM 115612, loc. 24-b; paratype cranidium, USNM 115613, loc. 24-b.

Genus MENOMONIA Walcott 1916

MENOMONIA CALYMENOIDES (Whitfield)
Plate 47, figure 7

Conocephalites calymenoides WHITFIELD, 1878, Wisconsin Geol. Survey, Ann. Rpt. for 1877, p. 52; WHITFIELD, 1882, Geology of Wisconsin,

vol. 4, p. 179; CHAMBERLIN, 1883, Geology of Wisconsin, vol. 1, p. 131; WHITFIELD, 1899, New York Acad. Sci. Annals, vol. 12, p. 182.
Ptychoparia calymenoides (Whitfield). WALCOTT, 1884, U. S. Geol. Survey Mon. 8, p. 48; VOGDES, 1893, California Acad. Sci. Occ. Papers, vol. 4, p. 348.
Menomonia calymenoides (Whitfield). WALCOTT, 1916, Smithsonian Misc. Coll., vol. 4, p. 348.

Original description.—(Description of cranidium only is given since no thoracic segments found with Warrior specimens described below.)

Species less than medium size, the largest head noticed measuring scarcely three-eighths of an inch in length. The glabella and fixed cheeks, the only parts of the carapace positively identified, present much the general appearance of a species of *Calymene*. Glabella proportionately small, not exceeding half the entire length of the head, conical in form and obtusely pointed above, the width across the base rather more than equalling half the length, separated from the fixed cheeks by deep, abrupt dorsal furrows, surface convex, prominent, destitute of glabellar furrows; frontal limb nearly twice as wide between the suture lines as the greatest width of the glabella, its surface elevated into a highly convex, transversely oval boss or tubercle, which is separated from the glabella by a wide, deep furrow; fixed cheeks highly and abruptly elevated, of proportionately large size, palpebral lobes semilunate or crescentiform and situated opposite the upper end of the glabella; occipital furrow narrow but deeply depressed; ring narrow, rounded and prominent. Facial suture nearly straight in front of the eye lobes to the middle of the tuberosity of the frontal limb around the front of which it seems to curve; behind the eye it is directed outward for nearly half the width of the lateral limb where it changes abruptly, forming an obtuse angle, and is then directed outward and backward with a slightly convex curvature of the posterior margin of the head at a point distant from the dorsal furrow about equal to the length of the glabella and occipital ring, forming large, triangular lateral limb.

The tuberosity of the frontal limb, the large, elevated fixed cheeks, deep dorsal furrows, and small size are prominent features and will serve to distinguish it from any known species.

Remarks.—The three cranidia assigned to this species came from the same locality and average about 2.0 mm. in length. The generic description calls for "three pairs of short lateral (glabellar) furrows" which are visible on two of the three cranidia. The present specimens, rather than showing "tuberosity of the frontal limb" agree with Lochman's Bonneterre material since the brim in both cases is smooth and concave. Only fragments of the characteristic "oval boss" are preserved. In referring to the Bonneterre specimens of this species, Lochman described "the fixed cheeks, glabella, and frontal border" as "covered with small granules and medium-sized granules with small central pits." The Warrior specimens show two rows of such relatively large pitted granules running approximately parallel on either side of the glabella. Sides of glabella smooth. Number of pitted granules in a row are four and these appear to be paired with those in the opposite parallel row. Occasionally, two granules occur close to each other or a granule may be found well out of line.

Occurrence.—Loc. 24-d.

Types.—Plesiotype, USNM 115644, loc. 24-d.

Genus MODOCIA Walcott 1924

Original description.—"The genus *Modocia* is established to include species with wide fixed cheeks which were formerly referred to six different genera."

Remarks.—The width of fixed cheeks of species described under this genus varies from more than one-half (*M. centralis*) to three-fourths (*M. yellowstonensis*) the width of the glabella.

MODOCIA BENORENSIS Tasch, n. sp.
Plate 46, figures 3–5

Cranidium semiovate with broadly conical, convex glabella, longer than wide, no glabellar furrows visible; fixed cheeks slightly more than one half width of the glabella, convex; palpebral lobes not preserved; ocular ridge raised, diagonal across fixed cheek; brim same width as frontal margin, convex, terminates in shallow, arcuate marginal furrow; border rounded forward, lower than brim; occipital furrow deeply indented across base of glabella, slightly arched near center of base of glabella, almost as wide as the occipital ring; occipital ring rounded, narrow, of greater height above base of glabella posteriorly.

Free cheek on far side has raised border about same width as frontal border, complete extension not preserved, probably tapers to genal spine; ocular platform rises with convex curvature from shallow furrow which extends entire length of border.

Facial suture cuts frontal border well out to side, curves out slightly to marginal furrow then proceeds backward to palpebral lobe with slight convexity, curves around palpebral lobe and proceeds diagonally outward and downward to within the genal angle.

Pygidium semicircular to suboblong in shape. Tapered axis with seven segments and terminal node. Pleural lobes convex, separated from axis by shallow furrow, segmentation not preserved; ends of pleura and axis form concave merger with short margin, axis does not extend beyond pleura. In lateral profile view, axis rises slightly above pleural lobes and merges with margin forming a 45° curve, and having greater concavity posteriorly.

Remarks.—*M. benorensis* differs from *weedi* and *centralis* in the absence of glabellar furrows and, from the latter, in the absence of an occipital spine; from *yellowstonensis* in narrower fixed cheeks and in having a brim and border of equal width.

Occurrence.—Rare in present collection. Loc. 107-k (7291, Bellefonte Quadrangle).

Types.—Holotype cranidium and pygidium, USNM 115609, loc. 107-k.

Genus PEMPHIGASPIS Hall 1863

Original description.—"The general form of the part of the shield known is semi-elliptical, rounded behind, nearly straight in the middle, in front, and becoming rounded towards the outer margin, distinctly trilobate. Axis narrow, straight, slightly narrow posteriorly, distinctly annulated; annulations direct. Lateral lobes ovate, extremely gibbous or ventricose, rising much above the axis; margins at the sides incurved."

Supplementary description.—General form of shield may vary from semi-elliptical to subcircular. Unexfoliated specimens have smooth exterior; lateral lobes show a variance in elevation above and below the axis, rising from slightly to very much above it, and to well below it.

Remarks.—*Pemphigaspis* is thus expanded to accommodate a new variety of *bullata* and a new species, *intermedia*, described below, and two other species, *inexpectans* Lochman, and *appalachia* Resser.

PEMPHIGASPIS BULLATA WADDLENSIS Tasch, n. var.

Plate 44, figure 13

Varies from *bullata* in a relatively slight rise of the lateral lobes over the axis and the gentler slope of lateral lobes towards axis.

Remarks.—Dr. Charles Butts (1936, p. 14) reported *Pemphigaspis* cf. *bullata* Hall from the Warrior formation. The new variety is probably identical with the form Butts reported.

Occurrence.—Rare in present collection. Three-quarters of a mile south of Waddle crossroads.

Types.—Holotype, USNM 115629, Old Quarry.

PEMPHIGASPIS INTERMEDIA Tasch, n. sp.

Plate 46, figures 10, 11

Lateral lobes fall below the axis which (lateral profile view) rises as a ridge above it.

Relationships.—In this feature *intermedia* differs from previously described species and can readily be identified by it. In all other characters it is like *bullata*.

Remarks.—Species based on two pygidia excellently preserved though both lack the complete right lateral lobe.

Occurrence.—Loc. 7294; 7341 Bellefonte Quadrangle.

Types.—Syntype, USNM 115630, loc. 7294; 7341.

Genus TRICREPICEPHALUS Kobayashi 1935

TRICREPICEPHALUS ARCUATUS Tasch, n. sp.

Plate 45, figures 9–12

Cranidium rectangular in outline, holotype one millimeter longer than greatest width, with convex, narrowly conical glabella, faint, line-like ridge along vertical median line, three pairs of furrows faintly indented on left side of glabella; dorsal furrow narrow, broad and V shaped from side of glabella to fixed cheeks, defines glabella on three sides; occipital furrow continuous, broad, displays gentle concave curvature in lateral profile view, slightly arched towards middle; occipital ring slightly wider than occipital furrow near midpart; middle portion not preserved.

Posterolateral limbs shorter than width of base of glabella, convex, broad intramarginal furrow, widening towards margins.

Fixed cheeks two-thirds width of glabella; palpebral lobe bean-shape, curved outward and backward, begins opposite median portion but extends to posterior third of glabella; palpebral furrow broad, clearly indented; ocular ridge extends diagonally across fixed cheeks from outer side of the dorsal furrow; brim of holotype between 2 and 3 mm. wide; in lateral profile view brim diagonal-like, terminating in marginal furrow; marginal furrow broad, shallow, with three narrow pits elongated in direction of furrow, middle pit situated along median line of glabella; its distance from pits on either side varies from 2 mm. in smaller cranidia, to 4 mm. in larger ones. Border slightly wider than brim, arcuate in outline, with broad crest along median line, rises steeply from marginal furrow and midway is thrust forward at low angle, peripheral portion slightly higher in elevation than posterior of brim.

Free cheeks unknown. Facial suture cutting anterior margin very near center, proceeds diagonally out and back briefly to marginal furrow, thence straight down and out curving around palpebral lobe, then running inward in broad curve, concave outward to cut posterior margin just within genal angle.

Brim, border and fixed cheeks pustulate.

Associated pygidium heavy, square in outline; axial lobe high, wide, gently tapered to broadly rounded terminus, divided into two wide segments and terminal portion by deep furrows; pleural lobes low, slightly more than one-half width of axis, gently convex, vertical; marginal border not preserved, except where terminal portion of axis merges with the continuation of the margin, the connection forms a concave curve; pleural lobes merge at posterolateral corners into bases of strong, long, curved spines that are directed upward at angle of approximately sixty degrees from the horizontal.

Exterior of axis pustulate; spines covered with irregular concentric venation, and line-like ridges curved along cross-sectional diameter of spine.

Relationships.—This species differs from the *tripunctatus* group of species in the nature of its border which is gently arched instead of sharply pointed. It appears to have closest affinity to *T. rex.* but differs from it in the greater convexity of its glabella, greater width of fixed cheeks, and marginal furrow, the shape of its brim and in axial segmentation and pygidial spines.

Remarks.—Species is based on a well-preserved internal mold and four external casts of cranidia and one pygidium, collected from the same horizon near the top of the Warrior.

Occurrence.—Loc. 13.3.

Types.—Holotype cranidium and associated pygidium, USNM 115623, loc. 13.3.

WELLERASPIS cf. NEWFOUNDLANDENSIS Lochman

Plate 45, figure 13

Remarks.—*W. newfoundlandensis* was set up on a single incomplete specimen. It is curious that a single specimen of this kind is known from the Smithsonian material. The glabella, glabellar furrows, and fixed cheek all conform to those of *newfoundlandensis.* Since occipital ring, brim, and posterolateral limbs are not preserved, the affinity suggested by the parts of the cranidium that are present cannot be pursued to a definite conclusion.

Occurrence.—Loc. 24-b.

Figured specimen.—Cranidium, USNM 115647, loc. 24-b.

BRACHIOPODA

Genus ACROTRETA Kutorga 1848

ACROTRETA sp. undet.

Plate 45, figure 8

Genus *Acrotreta* Kutorga, WALCOTT, 1912, U. S. Geol. Survey Mon. 51, pp. 671–672.

Walcott's revised description of the genus (abridged).—"Ventral valve strongly convex to conical, with posterior face more or less flattened to form a false area that is usually marked by a shallow, median groove. Pedicle opening at the apex of the cone and directed more or less backward. Apex usually anterior to the posterior margin but usually overhanging it."

Remarks.—A single well-preserved ventral valve, 11 mm. in length, is assigned to this genus. Since the flattened posterior face is covered from view, the presence of a shallow median groove that marks the false area cannot be determined and hence specific determination cannot be made. The

high apex projects less than one millimeter beyond the base of the valve which is approximately 11 mm. wide. Matthew (1903), in his description of *Acrothyra proavia*, noted that this species differed from the Acrotretinae in that "the high overhanging apex" projected from one-quarter to one-third beyond the base of the valve. Accordingly, the specimen described here cannot be assigned to *Acrothyra* and is assigned to *Acrotreta*.

Occurrence.—Loc. 24-b.

Figured specimen.—Ventral valve, USNM 115626, loc. 24-b.

Genus LINGULELLA Salter 1866
LINGULELLA cf. MARCIA Walcott
Plate 45, figure 7

Lingulella marcia WALCOTT, 1911, Smithsonian Misc. Coll., vol. 57, no. 4, pp. 74–75, pl. 14, fig. 3–3a; 1913, Research in China, vol. 3, p. 69, pl. 2, fig. 6a.

Original description.—"One of the small forms allied to the groups of similar shells mentioned under *L. manchuriensis*. It differs from the latter species in being relatively broader in outline, with the sides of the valves less uniformly arched, and in having a more broadly rounded frontal margin."

Remarks.—A single partly exfoliated dorsal valve shows closest affinities to *marcia*, a brachiopod described from the Middle Cambrian Fu-chou series of Manchuria.

Occurrence.—Loc. 24-d.

Figured specimen.—USNM 115625, loc. 24-d.

Genus LINGULEPIS Hall 1863
LINGULEPIS ACUMINATA (Conrad)
Plate 45, figure 18

Lingulella (*Lingulepis*) *acuminata* (Conrad), WALCOTT, 1912, U. S. Geol. Survey Mon. 51, part 1, p. 545, pl. 40, fig. 1-p; pl. 42, fig. 1-c.

The individuals of the species described here are represented by the narrow form of the ventral valve which is acuminate and has a length of 11 mm., and by a single ovate dorsal valve.

Relationships.—*L. acuminata* may be distinguished from *nabis*, with which it has closest affinities, by the greater length and greater curvature of its lateral margins and by its dorsal valve which is ovate rather than elongate.

Occurrence.—Loc. 24-d.

Types.—Plesiotype, ventral valve, USNM 115627, loc. 24-d.

Genus MICROMITRA Meek 1873
MICROMITRA ALABAMENSIS (Walcott)
Plate 45, figure 6

Iphidea alabamensis WALCOTT, 1897, U. S. Nat. Mus. Proc., vol. 19, pp. 713–714, pl. 59, figs. 5, 5a–b.

Micromitra alabamensis (WALCOTT), 1912, U. S. Geol. Survey Mon. 51, part 1, p. 337, pl. 2, figs. 5, 5a–c.

Supplementary description.—Ventral valve moderately convex; highest point being broadly rounded umbo above line of valve junction; no other parts except surface preserved. Surface marked by elevated concentric growth ridges. These are underlain by barely distinguishable radiating costellae which cause the tendency to crenulation of the striae noted by Walcott as the chief specific character. The costellae are not visible except when placed at a favorable angle under the binocular microscope. Entire surface of valve a dull black.

Occurrence.—Loc. 24-d, 107-k, 12.45.

Types.—Plesiotype, ventral valve, USNM 115624, loc. 24-d.

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ADDENDUM

After this report was completed and while it was awaiting publication, certain additional material became available.

During the summer of 1950, the writer collected trilobites from the upper part of the section near Warriorsmark, Pennsylvania (Butts' locality 24-f). *Cedaria* zone forms typical for the Waddle section were found. No *Crepicephalus* zone forms are included in this material.

Dr. James Lee Wilson (personal communication) found, upon restudy of the trilobites he collected at the Old Quarry, that a previously identified *Crepicephalus* trilobite was a *Coosella* species, and that the rest of the fauna at that locality included the following genera: *Welleraspis*, *Kingstonia*, *Maryvillia*, *Blountia*, *Nixonella* (?), *Bolaspidella*, *Millardia*. Since this fauna has a *Cedaria* zone cast, this would favor the view that the beds of the Old Quarry are stratigraphically below exposure Number 11 and that no faulting occurred. However, a pemphigaspid trilobite in the Pennsylvania State College collections reportedly came from the Old Quarry. If so, this occurrence would be anomalous and require explanation since as Dr. Wilson further observes, neither *Crepicephalus* nor *Pemphigaspis* species have been found below the upper 300 feet of the Warrior.

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JOURNAL OF PALEONTOLOGY, VOL. 25, NO. 3, PP. 307–320, PLS. 48–50, 1 TEXT FIGURE, MAY 1951

NONMARINE OSTRACODES—THE SUBFAMILY CYPRIDEINAE IN THE ROCKY MOUNTAIN AREA

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ABSTRACT—All known species of the Cyprideinae (*Cypridea* s. l.) from the Rocky Mountain area are described, illustrated, and their stratigraphic distribution discussed. The genus *Ulwellia* Anderson is recorded for the first time from North America and the genus *Pseudocypridina* Roth is redefined. Five new species are described.

THIS is the first of a series of proposed papers on the micropaleontology of the nonmarine formations of the Rocky Mountain area. There have been several papers on this subject by Jones (1886, 1893), Roth (1933), Harper and Sutton (1935), Peck (1937, 1941), and Swain (1949). Mrs. Betty Kellett Nadeau has in preparation an extensive paper on the Morrison ostracodes. In the present series the writer will describe family or generic units of microfossils with emphasis on their stratigraphic distribution. The ostracode subfamily Cyprideinae (*Cypridea* Bosquet, s. 1.) was chosen as the first group to receive monographic treatment because this subfamily is so well represented, and because representatives of the Cyprideinae have been used with success in zoning the Purbeck-Wealden of England and northern Europe (Martin, 1940, Sylvester-Bradley, 1949, Wolburg, 1949). Papers in preparation deal with the metacyprids and the charophytes.

The writer has had an unusual opportunity to obtain large collections of well preserved microfossils from this area. The Geological Society of America furnished field expenses for collecting in the summers of 1938 and 1941, many specimens have been submitted by colleagues, and considerable collecting has been done by graduate students engaged in field work at the University of Missouri Camp Edwin B. Branson near Lander, Wyoming.

Contrary to popular belief, the microfossils (ostracodes and charophytes) of the nonmarine formations are well preserved, are sufficiently varied that they can be easily arranged in specific categories with definite stratigraphic significance, and, if sought in calcareous shales and shales in association with the nonmarine limestones, are surprisingly abundant. The work done with them to date has been largely of a reconnaissance nature, collections having been made primarily to verify occurrence and distribution. Even so, the microfossils indicate definitely that the lithologic unit known as the Morrison formation transgresses the Jurassic-Lower Cretaceous boundary to the northwest from eastern Wyoming (Peck and Reker, 1948), and that the Gannett group of western Wyoming and eastern Idaho, the Kootenai of central Wyoming, the Lakota-Minnewaste formations of the Black Hills region, and parts of the Trinity of the Gulf Coast contain distinctive nonmarine microfossils that make their correlation much more positive. More detailed collecting is certain to produce results in establishing closer age relationships and in giving an insight on paleogeographic conditions.

In preparing this paper the writer has made an attempt to heed the pleading of Dr. Aldrich of the Geological Society of America and other editors, to boil down and reduce the number of words used. Most paleontologists, including the writer, have made a practice of telling everything they can find out about a species, regardless of whether or not they were repeating ordinal, familial, and generic characters in a specific description. In this paper a synonymy, a very brief diagnosis, and an illustration or two showing the chief specific characters, are given for each previously described species. On new species an attempt is made to give as many illustrations as necessary to show specific characters and the indi-

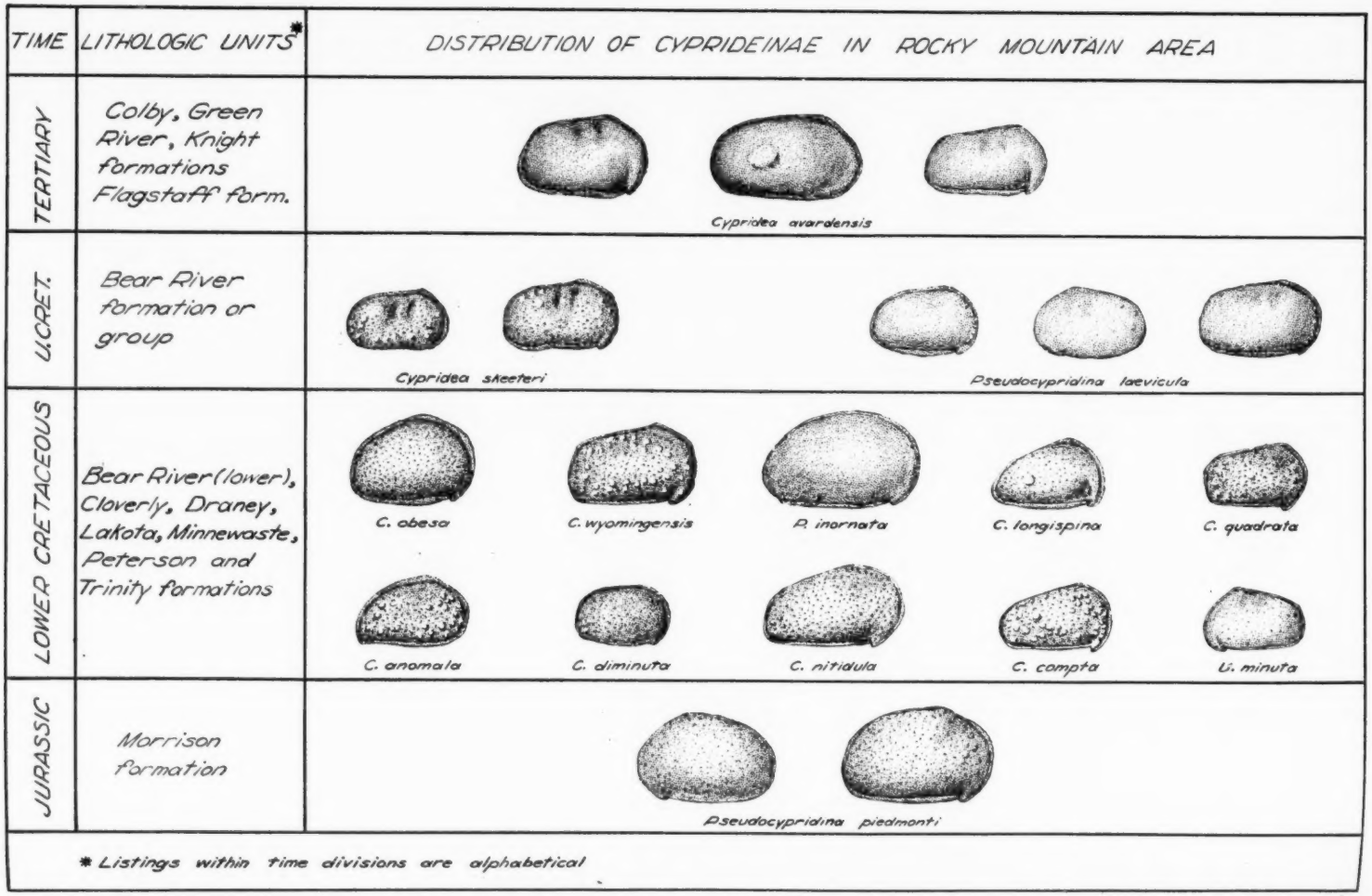


FIG. 1—Distribution of Cyprideinae in formations of the Rocky Mountain area.

vidual variations within a species. The description has been written primarily to supplement the illustrations and only characters used to identify the species and differentiate it from other species of that genus are given. To aid identification brief diagnoses of genera are included.

The illustrations are camera lucida drawings on Ross board and were prepared by Vaona Hedrick Peck. Mrs. Betty Kellett Nadeau has read the manuscript and made many helpful suggestions. A major part of the collecting was done by the writer under Geological Society of America Research Grant No. 354–40. Thanks are due Mr. W. W. Skeeters of the Mountain Fuel Supply Co., Rock Springs, Wyoming, for furnishing specimens from localities in southwestern Wyoming, and to many colleagues and students that have contributed specimens, stratigraphic information, and advice on systematic problems.

STRATIGRAPHIC DISTRIBUTION

The Cyprideinae in North America occur in restricted localities of the Jurassic Morrison formation, are widely distributed and abundant in the nonmarine Lower Cretaceous formations, and are present but localized in the Upper Cretaceous and Tertiary formations (figure 1). It is probable that the localized distribution in the Upper Cretaceous means a lack of collecting rather than an absence of fossils.

The only representative of the Cyprideinae in the Jurassic of the Rocky Mountain area is *Pseudocypridina piedmonti* Roth, a common and characteristic species of the Morrison of the Black Hills region. It occurs with ostracodes and charophytes that are widely distributed in the Morrison in southwestern Wyoming, Colorado, and New Mexico, but neither *P. piedmonti* nor any other representative of the Cyprideinae has been described from the Morrison outside of the Black Hills area. This fact supports the conclusion reached by Betty Kellett Nadeau in her study of the entire Morrison ostracode fauna: "The Morrison of the Black Hills area is middle or upper Morrison and the lower part, as represented at the type locality, is not present in the Black Hills area" (personal communication).

In the Lower Cretaceous formations the Cyprideinae, with the metacyprids, are the dominant ostracodes in numbers and species. *Pseudocypridina inornata* (Peck), obviously a descendant of *P. piedmonti* and closely related to it, is widespread in the Lower Cretaceous. *Cypridea longispina*, *C. anomala*, *C. compta*, *C. wyomingensis*, *C. nitidula*, and *C. quadrata* are all widely distributed and abundantly represented species that make excellent Lower Cretaceous markers. In the restricted occurrence of the Minnewaste limestone of the Black Hills, the only known North American representative of the genus *Ulwellia* Anderson is found.

Cyprideinae are abundant in the Bear River formation of southwestern Wyoming and are represented by the smooth glossy carapaces of *Pseudocypridina laevicula*, and the oldest representative of the Cyprideinae to possess well developed sulci, *Cypridea skeeteri*. The restricted distribution and paucity of species in the Upper Cretaceous is probably more apparent than real. The writer has had little opportunity to collect from the Upper Cretaceous Laramie but can see no reason why Cyprideinae should not be well represented there.

In the Tertiary the Cyprideinae are represented by a single species, the widespread and abundant *Cypridea arvadensis* (Swain). This species ranges from Flagstaff limestone of probable Paleocene age to the Eocene Green River formation.

COLLECTING LOCALITIES

Lower Cretaceous

1–27. Descriptions of localities 1–27 have been published (Peck, 1941). In general these localities are as follows:
  1–3. Lower part of the Bear River formation of western Wyoming.
  7–21. In and near the Peterson and Draney limestones of the Gannett group in western Wyoming and eastern Idaho.
  22–27. Limestones and calcareous shales of the Kootenai formation in central and central-western Montana.

28. Minnewaste limestone in Calico Canyon, south of Buffalo Gap in SE ¼, sec. 24, T. 6 S., R. 6 E., Custer County, South Dakota.

29. Minnewaste limestone-shale partings in exposure on Skyline Drive, east of Hot Springs, Fall River County, South Dakota.

30. Lakota formation—gray to almost black shale lens exposed on north side of Fall River Road 3.2 miles southeast of Hot

FIG. 1—Distribution of Cyprideinae in formations of the Rocky Mountain area.

Springs, Fall River County, South Dakota. Shale is about 15 feet thick and rests on the Unkpapa sandstone.

31. Cloverly—shales above and below fairly massive limestones weathering platy and containing many gastropods, in variegated beds at Devils' Slide, 5 miles north of Gardner, Montana, on the west side of the Yellowstone River Valley.
32. Cloverly formation—approximately 4 miles west of Lander, Wyoming, on the north side of Baldwin Creek, in the S ½ SE ¼, Sec. 5, T. 33 N., R. 100 W., Fremont County, Wyoming. Samples taken from shales associated with dense limestone beds above lowest varicolored beds and about fifteen feet below the prominent conglomerate. Number 4 of measured section (Peck and Reker, pp. 127, 132, 1948).
33. Cloverly formation—approximately 3 miles southwest of Lander, Fremont County, Wyoming, about halfway between the roads in Squaw Creek and Middle Fork of the Popo Agie River. Samples taken near dense limestone at same stratigraphic position as locality 32.

33a. Cloverly formation—northwestern end of Lander anticline about 2 miles north of Lander, Fremont County, Wyoming. Sample taken in shales under limestone in the upper part of the formation.

Jurassic

34. Morrison formation—road cut on Highway 24A, 7 miles north of Whitewood, Lawrence County, South Dakota. Samples taken in lower 50 feet of exposure from light gray calcareous sandy clays and shales in association with thin beds of limestone.
35. Morrison formation—road cut on Highway 24, 6 miles west of Whitewood, Lawrence County, South Dakota. Sample taken in dark gray shales with thin limestones just under the Morrison-Lakota contact.
36. Morrison formation—3 miles due north of Piedmont, Meade County, South Dakota. Samples containing excellent ostracodes and charophytes were taken (numbers correspond to measured section on page 11 of the Black Hills folio 219) from (a) near a thin lenticular fossiliferous limestone in the "20 feet of gray to blue shale" directly below the Lakota (number 3); (b) from 20 feet of shale containing limestone layers, (number 7); and (c) the nodular limestone layers near the base (number 9).

Cretaceous

37. Bear River formation on Sulphur Creek, Sec. 29, T. 14 N., R. 119 W., 9 miles southeast of Evanston, Uinta County, Wyoming. Samples taken in calcareous shale beds and shale partings.
38. Bear River formation in Shell Hollow, E ½ of SE ¼ of Sec. 12, T. 16 N., R. 121 W., 7 miles north of Evanston, Uinta County, Wyoming. Samples taken in calcareous shale beds and shale partings.

38a. Bear River formation at Spring Creek Gap in the E ½ Sec. 30, T. 16 N., R. 117 W., Uinta County, Wyoming. Samples taken by W. W. Skeeter in the upper 250 feet of the formation.

38b. Bear River formation on Fish Creek in the NE ¼ Sec. 36, T. 30 N., R. 115 W., Sublette County, Wyoming. Samples taken by W. W. Skeeter.

Paleocene

39. Flagstaff limestone one mile east of Ephraim, Utah. Shale partings in excellent exposure of the limestone (localities 7–10 of Swain, 1949).

Eocene

40. Douglas Creek member of the Green River formation on the south side of Douglas Creek Pass, Garfield County, Colorado. Composite sample of shale partings in sandy limestone in a road cut near the base of the formation.
41. Green River, lower part, 10 miles east of Kemmerer, Wyoming, in road cut on north side of U.S. Highway 30. Sample taken in a zone of fossiliferous limestone and siltstone.
42. Knight formation probable, 6 miles east of Kemmerer in a road-cut on the north side of U.S. Highway 30. Sample taken in greenish fossiliferous calcareous sandstone and shale (locality 25 of Swain, 1949).
43. Colton formation, 8 miles north of Castlegate, Utah, on Highway 33. Sample taken near the above fossiliferous mudstone in road cut (locality 11 of Swain, 1949).

SYSTEMATIC DESCRIPTIONS

Order OSTRACODA

Family CYPRIDAE

Subfamily CYPRIDEINAE Martin, 1940

Cypridae with a distinct beak and notch located between the anterior and ventral borders.

Genus CYPRIDEA Bosquet, 1852

Genolectotype: Cypris granulosa Sowerby, 1836 (designated by Sylvester-Bradley, 1947).

Cyprideinae with the left valve the larger and overlapping the right. Surface of the valves distinctly pitted, and may bear granules, tubercules, and spines.

The genus *Cypridea* has been the subject of extensive and detailed discussions in recent years by Anderson (1939), Martin (1940), Swain (1946) and Sylvester-Bradley (1949). The writer can add little to the

details of morphology and structure as they have been described and illustrated in the above papers, but the disagreement on classification at the generic and subgeneric level is so great that some additional discussion is necessary.

Anderson (1939) subdivided the genus *Cypridea* into five genera and proposed to include in the subfamily Rostrocyprinae all Cypridae characterized by an antero-ventral beak and notch. Martin (1940) recognized the validity of the subfamily but pointed out that Anderson had violated the Rules of Nomenclature in forming the subfamily name. Martin substituted the subfamily name Cyprideinae and included all of Anderson's new genera of this subfamily in the synonymy of *Cypridea*. For all practical purposes, Martin's subfamily Cyprideinae and the genus *Cypridea* as defined by him, are synonyms.

In 1949 Sylvester-Bradley reviewed the literature on the genus *Cypridea* and gave a thorough and complete description of the genolectotype, *Cypridea granulosa* (Sowerby). Sylvester-Bradley recognized the value of the generic names introduced by Anderson in 1939 but reduced them to subgeneric rank. In effect, Sylvester-Bradley followed Martin in making the subfamily Cyprideinae and the genus *Cypridea* synonymous in meaning.

The writer does not believe that any useful purpose is served by the subgeneric names and trinomial nomenclature that has been proposed for the Cyprideinae. If the Cyprideinae include all Cypridae with an antero-ventral beak and notch, then the genus *Cypridea* should, in order to serve a practical purpose, be restricted to a subdivision of the subfamily.

In studying the North American representatives of the Cyprideinae the writer has come to the conclusion that several of the subdivisions of *Cypridea* s. l. are valid genera. These are *Cypridea* Bosquet s. s. as defined by Sylvester-Bradley (1949), *Ulwellia* Anderson, and *Pseudocypridina* Roth of which *Langtonia* Anderson is a synonym. As well as can be told from the fossil record these genera are monophyletic and the use of the names shows relationships and saves considerable repetition of detail in specific descriptions. *Morinina* Anderson and *Cyamocypris* Anderson have not been identified in the material included in this study and the writer has no opinion concerning their status.

CYPRIDEA ANOMALA Peck
Plate 49, figures 12, 13

Cypridea anomala PECK, 1941, Jour. Paleontology, vol. 15, p. 299, pl. 43, figs. 18–28.

Carapace subquadrate and strongly angular dorsally with greatly reduced or nonexistent beak and flattened ventral surface. Most specimens are nodose, the nodes scattered or grouped anteriorly and posteriorly.

Distribution.—Lower Cretaceous. Widely distributed and abundant in the Draney limestone and the lower part of the Bear River formation; Kootenai localities 26 and 27; Cloverly formation locality 31.

Types.—Univ. Missouri, holotype 0-973-1; paratypes 0-974-4.

CYPRIDEA BREVICORNIS Peck
Plate 49, figures 7, 8

Cypridea brevicornis PECK, 1941, Jour. Paleontology, vol. 15, p. 299, pl. 44, figs. 22–24.

Carapace small, subovate. A short, blunt spine present just posterior to and above the center of each valve, and back of the spine on a few specimens are irregularly scattered nodes.

Distribution.—Lower Cretaceous. Draney limestone at localities 6, 7, 9, 13, and 14.

Types.—Univ. Missouri, holotype 0-977-5; paratypes 0-976-1.

CYPRIDEA COMPTA Peck
Plate 49, figures 1–4, 14

Cypridea compta PECK, 1941, Jour. Paleontology, vol. 15, p. 300, pl. 44, figs. 25–28.

Small, subovate *Cypridea* with variable number of nodes, the nodes concentrated around the outer parts of the valves, leaving the centers free, except for a large, subcentral node present on some specimens.

Distribution.—Lower Cretaceous. Draney formation at localities 5, 6, 9, and 11; lower part of the Bear River formation at locality 3a; Cloverly formation at localities 32 and 33a.

Types.—Univ. Missouri, holotype 0-976-5; paratypes 0-975-1.

CYPRIDEA DIMINUTA Vanderpool
Plate 49, figure 6

Cypridea diminutus VANDERPOOL, 1928, Jour. Paleontology, vol. 2, p. 103, pl. 13, figs. 7, 8.
Cypridea diminuta, PECK, 1941, Jour. Paleontology, vol. 15, p. 298, pl. 44, figs. 29–32.

Carapace small to medium size for the genus, rectangular in outline. Beak and notch inconspicuous to absent.

Distribution.—Lower Cretaceous. Rare in the Draney formation at localities 6, 14, and 18. Reported by Vanderpool (1928) as common in the De Queen and Glen Rose formations of Arkansas and Texas.

Types.—Holotype, number 504 of Micropaleontological Collection of the University of Oklahoma; figured specimen, Univ. Missouri, number 0-976-2.

CYPRIDEA LONGISPINA Peck
Plate 48, figures 12–15

Cypridea longispina PECK, 1941, Jour. Paleontology, vol. 15, p. 300, pl. 43, figs. 6–9.

Species characterized by small size, strong posterior slope of hinge line, strong overlap by the left valve, and the possession of a prominent spine on the posterior portion of each valve. On some specimens the spine is broken and on a few of the smaller specimens there is no evidence of its occurrence.

Distribution.—Lower Cretaceous. Abundant in Kootenai at locality 23 and in Lakota at locality 30. Comparatively rare in the Cloverly near Lander, Wyoming, at locality 32.

Types.—Univ. Missouri, holotype 0-975-5; paratypes 0-974-1.

CYPRIDEA NITIDULA Peck
Plate 49, figure 5

Cypridea nitidula PECK, 1941, Jour. Paleontology, vol. 15, p. 301, pl. 43, figs. 1–5.

Carapace fairly large, suboblong, with prominent anterocardinal angle, beak and notch.

Distribution.—Lower Cretaceous. Draney limestone at localities 4, 7, 9, and 14; lower part of Bear River formation at locality 3a.

Types.—Univ. Missouri, holotype 0-975-3; paratypes 0-975-4.

CYPRIDEA WYOMINGENSIS Jones
Plate 48, figures 5–7

Cypridea tuberculata var. *wyomingensis* JONES, 1893, Geol. Mag., decade 3, vol. 10, p. 386, pl. 15, figs. 5a, b; 6a, b.
Cypridea tuberculata var. *gypsumensis* VANDERPOOL, 1928, Jour. Paleontology, vol. 2, p. 103, pl. 13, figs. 9–12.
Cypridea wyomingensis PECK, 1941, Jour. Paleontology, vol. 15, p. 297, pl. 43, figs. 10–17.

Medium sized, somewhat angular species with surface of valves bearing numerous more or less irregularly placed nodes.

Distribution.—Lower Cretaceous. Common and widely distributed in the Draney limestone, Kootenai formation, and lower part of the Bear River formation. Also occurs in the De Queen clays of Arkansas (Vanderpool, 1928).

Types.—Location of primary types unknown, but probably in the British Museum. Figured specimens, Univ. Missouri 0-973-3-4, 0-1200-2.

EXPLANATION OF PLATE 48

All figures ×37. All specimens in the University of Missouri Collections.

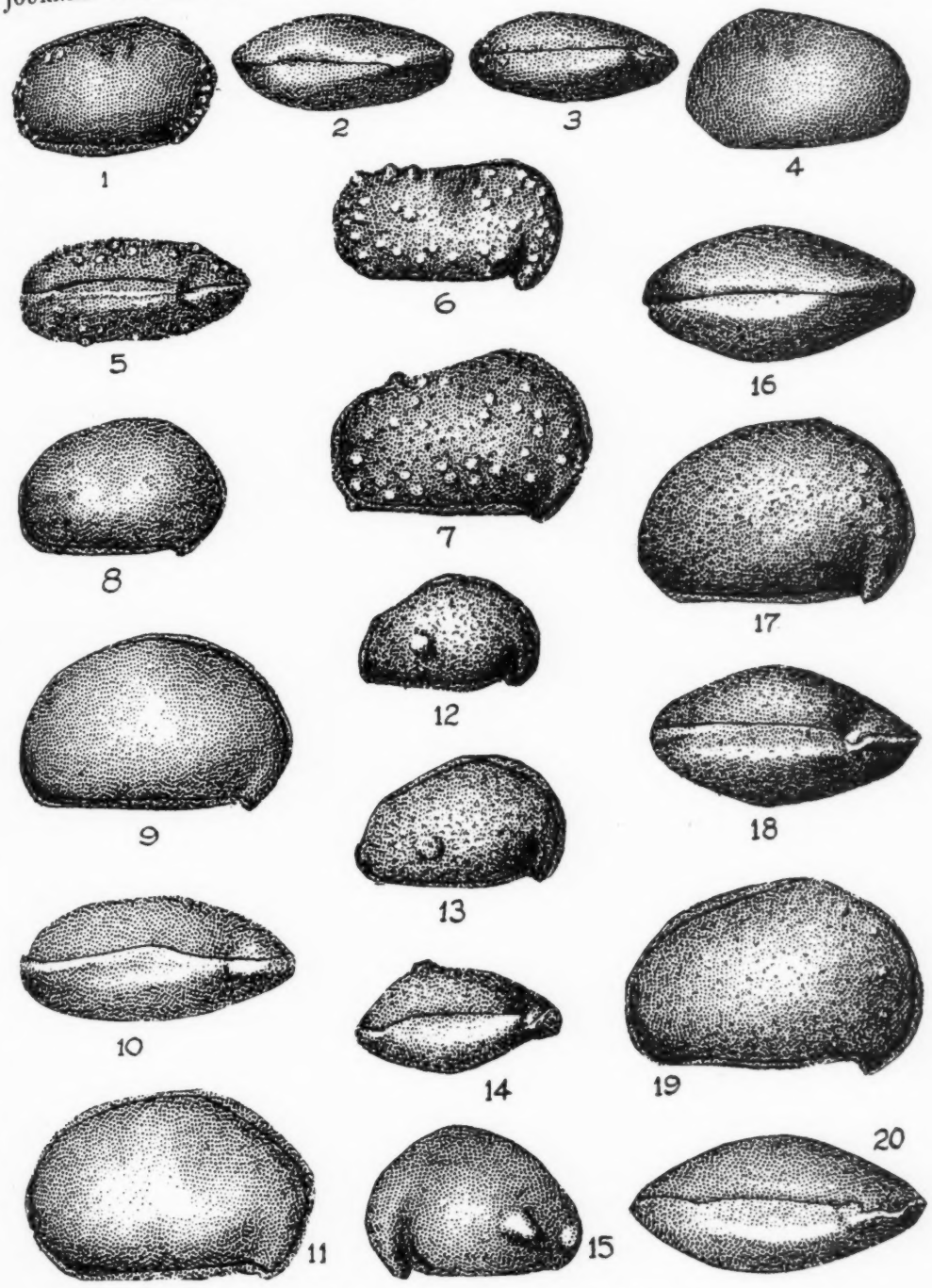
FIGS. *1–4*—*Pseudocypridina laevicula* Peck, n. sp., *1*, right valve of holotype, 0-1200-1; *2*, *3*, *4*, dorsal, ventral, and left valve views of paratypes, 0-1081-2-4. (p. 319)

5–7—*Cypridea wyomingensis* (Jones), *5*, ventral view showing overlap, 0-1200-2; *6*, right valve of elongate specimen 0-973-3; *7*, right valve of normal specimen, 0-973-4. (p. 312)

8–11—*Pseudocypridina inornata* (Peck), *8*, left valve of small specimen from the Minnewaste, 0-1200-3; *9*, right valve view of Lakota specimen, 0-1200-5; *10*, *11*, ventral and left valve views of Kootenai specimen, 0-1200-4. (p. 319)

12–15—*Cypridea longispina* Peck, *12*, right valve view of specimen from Lakota, 0-1201-1; *13*, *14*, right valve and ventral views of specimen from Cloverly, 0-1201-2; *15*, left valve of holotype from Kootenai, 0-975-5. (p. 312)

16–20—*Pseudocypridina piedmonti* Roth, *16*, *17*, *18*, dorsal, right valve, and ventral views 0-1201-5; *19*, *20*, right valve and ventral views of topotype, 0-1201-4. (p. 319)



Peck, Rocky Mountain Cyprideinae

CYPRIDEA ARVADENSIS (Swain)
Plate 50, figures 1–12, 16–18

Ilyocypris arvadensis SWAIN, 1949, Jour. Paleontology, vol. 23, p. 178, pl. 32, figs. 20–22, pl. 33, figs. 1–9.
Cypridea bisulcata SWAIN, 1949, Jour. Paleontology, vol. 23, p. 180, pl. 33, figs. 13–19.

Subquadrate to subovate, bisulcate, fairly large *Cypridea*, with anteroventral beak and notch small and inconspicuous to absent. Dorsal sulci fairly deep and conspicuous on small individuals up to about 1 mm. in length, above that size becoming broad and shallow and grading into the general outline of the carapace. Low nodes developed on the anterior and posterior lobes of a few individuals.

Remarks.—In 1949 Swain described *Ilyocypris arvadensis* and *Cypridea bisulcata* from the Paleocene and Eocene of the Rocky Mountain area, and pointed out that the two species constituted a remarkable example of isomorphism. According to Swain the two species can be distinguished only on the manner of overlap on the ventral surfaces.

After studying several hundred specimens, part of them topotypes, that would have to be assigned to either *I. arvadensis* or *C. bisulcata*, the writer has come to the conclusion that all of these ostracodes are representatives of the genus *Cypridea*, and that there is no more variation than would be expected among so many individuals in a species of this genus. The conspicuous variations are in the strength of the ornamentation, the prominence of the beak and notch, the prominence of the posterocardinal angle, and the amount and manner of overlap of the left valve along the ventral margin. By using all of these criteria the specimens here referred to *Cypridea arvadensis* could be divided into numerous species and subspecies, all of which would grade into each other by almost imperceptible stages.

The most conspicuous variation within these specimens is the presence or absence of a beak. When many individuals are examined it seems at first that the specimens could easily be divided into species or genera on the presence or absence of a beak. Closer examination and manipulation under light to vary the shadows discloses that many of the specimens that appeared beakless at first glance really possess a beak but it is so small that it is easily overlooked. Many specimens do not possess a beak, but complete series can be built up from the beakless forms to those with prominent beaks.

The amount and manner of the ventral overlap was used by Swain (1949, p. 180) to differentiate between the genera *Ilyocypris* and *Cypridea*. There is considerable variation in this character among the described species of *Cypridea*. Among the specimens under consideration, the forms without a beak or with the least prominent beaks are the forms on which the contact margins of the valves pass from the anterior margin

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EXPLANATION OF PLATE 49

All figures ×37. All specimens in the University of Missouri Collections.

FIGS. *1–4, 14—Cypridea compta* Peck, *1–3*, dorsal, right valve, and ventral views, *4*, right valve view of smaller specimen from the Cloverly, 0-1202-1; *14*, right valve of holotype from the Kootenai, 0-976-5. (p. 311)

5—Cypridea nitidula Peck, right valve of holotype, 0-975-3. (p. 312)

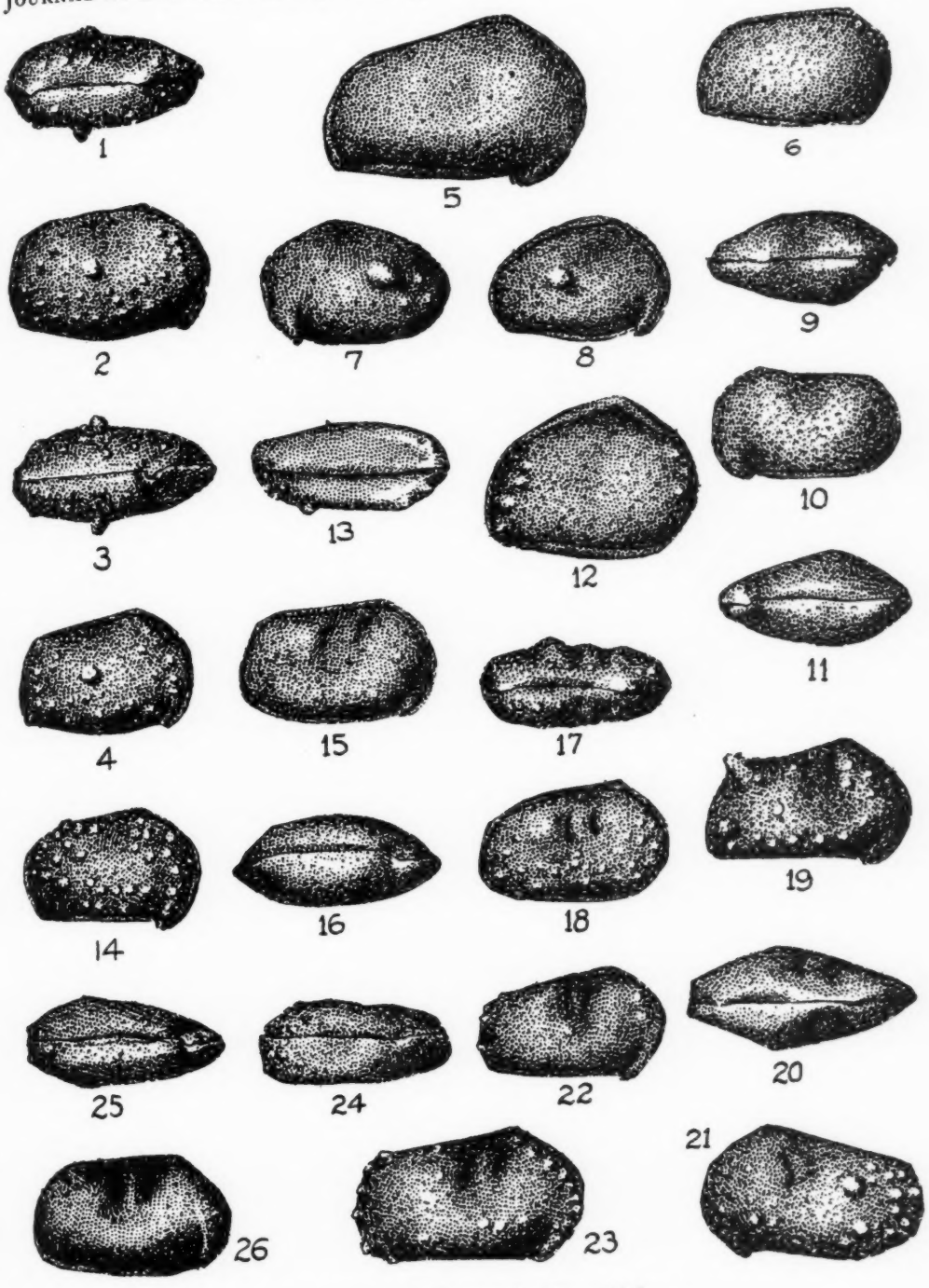
6—Cypridea diminuta Vanderpool, right valve, 0-976-2. (p. 312)

7–8—Cypridea brevicornis Peck, left and right valve views of holotype, 0-977-5. (p. 311)

9–11—Ulwellia minuta Peck, n. sp., dorsal, left valve, and ventral views of holotype, 0-1202-2. (p. 320)

12–13—Cypridea anomala Peck, *12*, right valve of holotype, 0-973-1; *13*, ventral view of paratype (right valve on top), 0-973-4. (p. 311)

15–26—Cypridea skeeteri Peck, n. sp., *15*, *16*, right valve and ventral views of thick paratype, 0-1084-2; *17*, *18*, dorsal and right valve views of beakless paratype, 0-1202-4; *19*, right valve view of paratype with post-dorsal spine, 0-1202-5; *20*, dorsal view of paratype, 0-1084-1; *21*, left valve of paratype with unusual number of nodes, 0-1080-2; *22*, right valve of small paratype, 0-1084-4; *23*, right valve of holotype, 0-1203-1; *24*, ventral view of beakless paratype, 0-1203-2; *25*, ventral view of paratype with prominent beak, 0-1084-3; *26*, right valve of thick paratype, 0-1203-3. (p. 316)



Peck, Rocky Mountain Cyprideinae

to the ventral margin in a sweeping curve. The more prominent the beak, the greater the angulation between the anterior and ventral margins. Studies of large series of specimens indicate that this character is also a gradational one with many intermediate stages.

More detailed collecting and more detailed stratigraphic knowledge may make it useful at some time in the future to divide the specimens here referred to *C. arvadensis* into subspecies. With the present state of knowledge there seems to be no stratigraphic or systematic justification for the division.

Cypridea arvadensis has more delicate ornamentation and shallower sulci than *C. skeeteri* n. sp. from the Bear River formation, the only other known bisulcate species of *Cypridea* in North America.

Types.—Holotype of *Ilyocypris arvadensis* Swain, U. S. National Museum 560251, paratypes 560245, 560250, 560252-60; holotype of *Cypridea bisulcata* Swain, U. S. National Museum 560264, paratypes 560265–70. Specimens figured in this paper, Univ. Missouri 0-1203-4-5, 0-1204-1-4.

Occurrence.—Common and fairly widespread in the fresh-water limestones and calcareous shales of the Paleocene and Eocene of the Rocky Mountain area. Localities 40–43.

CYPRIDEA SKEETERI Peck, n. sp.
Plate 49, figures 15–26

Carapace of medium size, averaging about 0.9 mm. in length, subquadrate and angular in lateral outline, bisulcate, surface coarsely pitted. Anterior margin evenly rounded, posterior margin rounded above and below, truncate medially. Ventral surface flat, dorsal margin sloping more or less strongly to the posterior from the high antero-cardinal angle.

Beak and notch conspicuous and prominent to inconspicuous or absent, ventral overlap strong. If beak is present the anterior margin joins the ventral margin at a distinct angle, where the beak is absent the junction is made in a sweeping curve.

Dorsal sulci comparatively deep, short, grading into the general valve surface above mid-height. Central lobe low, inconspicuous, anterior lobe swollen, posterior lobe somewhat swollen and, on some specimens, produced into a short, blunt spine. A row of papillae parallels the anterior and posterior margins on several specimens and low scattered nodes occur on the posteriors of some specimens. The posterior and dorsal nodes may be produced into spines.

Remarks.—The principal diagnostic features of *C. skeeteri* are the prominent and deep sulci, the coarsely pitted surface of the valves, and the occurrence of papillae or nodes. The only other described bisulcate species, *C. arvadensis* (Swain) has more shallow sulci, and the pitting of the valve surface is much finer and less conspicuous.

As described above, *C. skeeteri* encompasses a variety of shapes and ornamentation that would be unlikely with a lesser number of specimens. If an attempt is made to establish subspecies or species on the variations in shape or ornamentation, intermediate specimens are present that could be referred to one division on one character and another division on another character. It is believed that all the specimens here referred to *C. skeeteri* lived in the same environment at about the same time and

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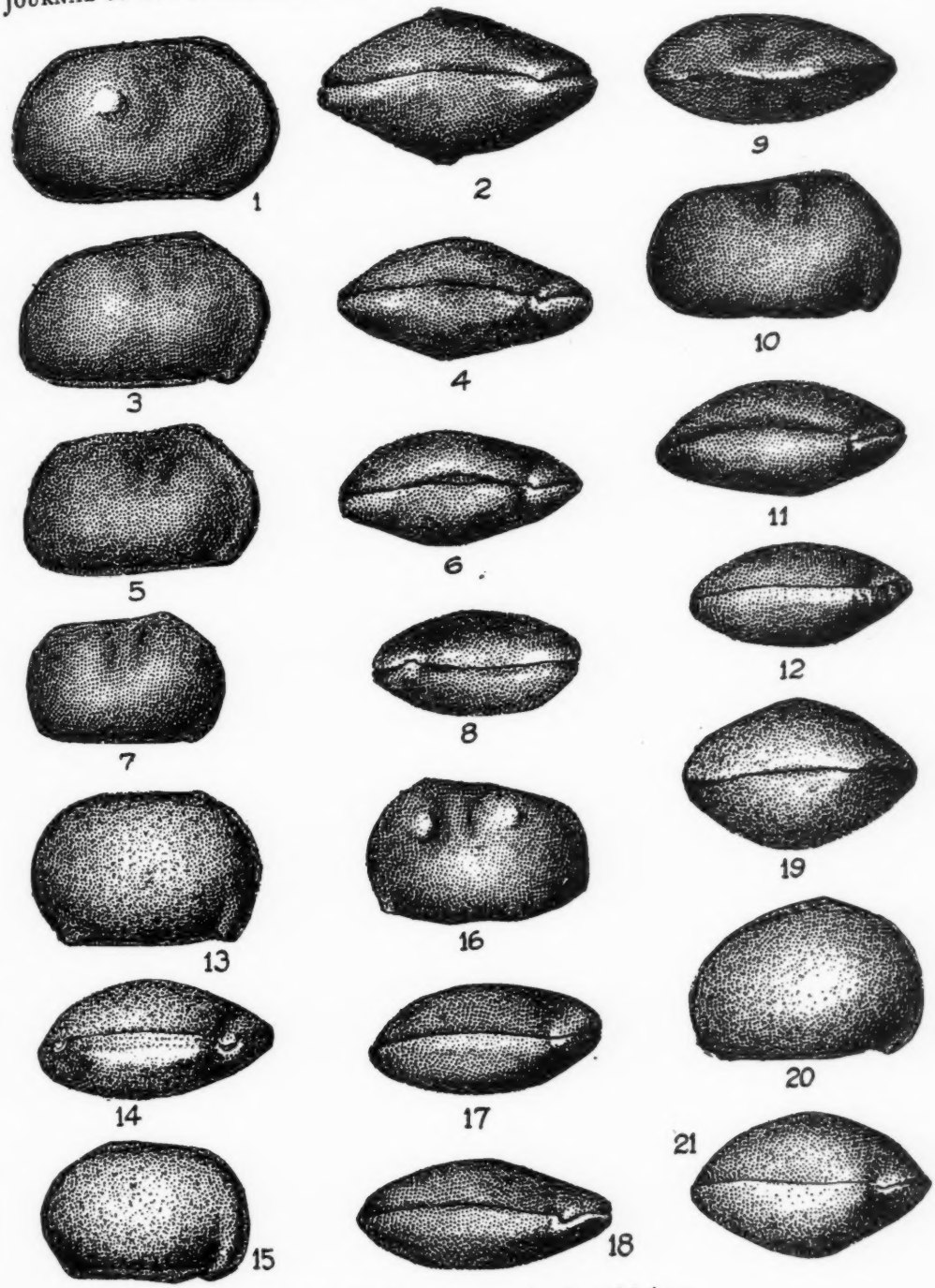
EXPLANATION OF PLATE 50

All figures ×37. All specimens in the University of Missouri Collections.

FIGS. *1–12, 16–18—Cypridea arvadensis* (Swain), *1–8*, right valve and ventral views of series of specimens showing range in size, variation in depth of sulci, and variation in prominence of the beak and effect of the beak on angulation at junction of ventral and anterior borders, 0-1203-4; *9, 10, 11*, dorsal, right valve, and ventral views of typical specimen, 0-1203-5; *12*, ventral view to show overlap and angulation, 0-1204-1; *16*, right valve of specimen with nodes, 0-1204-2; *17, 18*, ventral views to show angulation and overlap, 0-1204-3-4. (p. 314)

13–15—Cypridea quadrata Peck, n. sp., *13, 14*, right valve and ventral views of holotype; *15*, right valve of small paratype, 0-1205-2. (p. 318)

19–21—Cypridea obesa Peck, n. sp., dorsal, right valve, and ventral views of holotype, 0-1205-3. (p. 318)



Peck, Rocky Mountain Cyprideinae

probably could interbreed. The variations recognized are no greater nor more abundant than would be expected in a species of living animals.

C. skeeteri is another illustration of a species on which part of the specimens possess a well defined beak and notch and others show little evidence of a beak and notch. This set of conditions occurs several times within the Cyprideinae and, in the opinion of the writer, is an individual or, at the most, a subspecific character.

Distribution.—Cretaceous. Bear River formation at localities 37, 38, 38a, 38b.

Types.—Univ. Missouri, holotype 0-1203-1; paratypes 0-1202-4-5, 0-1203-2-3, 0-1084-1-4, 0-1080-2.

CYPRIDEA OBESA Peck, n. sp.
Plate 50, figures 19–21

Carapace of medium size, averaging about 1 mm. in length, strongly obese, and covered with small pits, the pits becoming aligned parallel to the long axis on the ventral surface. Hinge line sloping strongly to the posterior. Beak and notch small and inconspicuous but discernible on all specimens examined.

Remarks.—*C. obesa* is thicker in relation to its other dimensions than any other known species of *Cypridea*. The obesity, combined with the strongly sloping hingeline and ovate shape, make it a distinctive and easily identified species.

Distribution.—Lower Cretaceous. Cloverly formation near Lander, Wyoming, at localities 32 and 33.

Types.—Univ. Missouri, holotype 0-1205-3.

CYPRIDEA QUADRATA Peck, n. sp.
Plate 50, figures 13–15

Carapace of medium size, averaging about 0.9 mm. in length, quadrate in lateral outline with dorsal and ventral surfaces almost parallel. Surface coarsely pitted, with pits on the ventral surface in rows aligned with the long axis of the carapace. Beak and notch and posteroventral projection of the left valve well developed.

Remarks.—*C. quadrata* occurs in association with *C. obesa* in some localities and is differentiated from that species by shape in outline and by the relative thickness of the carapace.

Distribution.—Lower Cretaceous. Cloverly formation at localities 32, 33, and 33a. A single well preserved specimen was collected from near Manila, Utah.

Types.—Univ. Missouri, holotype 0-1205-2.

Genus PSEUDOCYPRIDINA Roth, 1933

Langtonia ANDERSON, 1939.

Genotype: Pseudocypridina piedmonti Roth, 1933.

Cyprideinae with the left valve the larger; carapace weakly pitted or smooth, beak weakly developed.

The genus *Pseudocypridina* was defined by Roth in 1933 to include those species differing from *Cypridea* in (1) not possessing a notch and (2) differing in size and position of the beak and in the general outline.

Two years later Harper and Sutton (1935) stated that Roth had failed to demonstrate the absence of a notch in his illustrations and description and that they considered it better to refer *P. piedmonti* Roth to *Cypridea*, pending further investigation. Martin (1940) included *Pseudocypridina* Roth in the synonymy of *Cypridea*.

Swain (1946) stated that specimens from Brazil resembled *P. piedmonti* Roth in all details, including the absence of an observable furrow or notch. Swain proposed that *Pseudocypridina* be redefined as a subgenus of *Cypridea* to include those specimens that "lack an anteroventral notch and hood" (Swain, 1946, p. 548). Sylvester-Bradley (1949, p. 146) agreed with Swain in assigning *Pseudocypridina* subgeneric rank to include those species of *Cypridea* with "left valve the larger; notch very slight or absent; beak much reduced; posteroventral projection of left valve very slight or absent; ornament weak or absent."

Examination of a large number of topotypes from Roth's locality and specimens from numerous localities in that vicinity has convinced the writer that many well preserved specimens of *P. piedmonti* do possess (1) slight and inconspicuous furrows or notches just posterior to the beak and (2) fairly strong, posteroventral projections

of the left valve. The beaks in representatives of *P. piedmonti* and other species referred to this genus are small and inconspicuous. There is considerable variation among specimens of *P. piedmonti* in prominence of the beak and notch, in the strength of the posteroventral projection of the left valve, and the smoothness of the curve of the dorsal, anterior, and posterior margins. These variations are to be expected when a large number of well preserved specimens are studied.

One character in which *P. piedmonti* consistently differs from most other Cypridеinae is in the weakness of the surface ornamentation. All well preserved specimens of *P. piedmonti* are faintly pitted. The pits are so difficult to distinguish on some specimens that careful manipulation under lights to obtain favorable shadows, or whitening the specimen with ammonium chloride powder is necessary to observe and study them. In the Lower and Upper Cretaceous of the Rocky Mountain area, and in the Jurassic and Cretaceous of Europe are other species with faintly pitted or smooth, glossy carapaces, and weak beaks. The establishment of a line of descent with weak ornamentation and weak beaks are characters that set apart in time and space a group of species that appear to be related and were first designated under the name *Pseudocypridina*.

PSEUDOCYPRIDINA PIEDMONTI Roth
Plate 48, figures 16–20

Pseudocypridina piedmonti ROTH, 1933, Jour. Paleontology, vol. 7, p. 404, pl. 48, figs. 7a–h.
Cypridea piedmonti, HARPER & SUTTON, 1935, Jour. Paleontology, vol. 9, p. 625, pl. 76, figs. 12–15.

Carapace fairly large, semicircular with strong anterocardinal angle, surface faintly pitted.

Remarks.—*P. inornata* (Peck) from the Lower Cretaceous is a closely related species, differing from *P. piedmonti* in possessing a smooth carapace with no pits and in having a less prominent anterocardinal angle. On selected specimens, the two species may appear identical, but studies of large suites indicate consistent differences.

Distribution.—Jurassic Morrison formation. Common in and restricted to the Morrison formation of the Black Hills region, South Dakota.

Types.—Holotype of *Pseudocypridina piedmonti* Roth, U. S. National Museum 74,473; figured specimens, Univ. Missouri 0-1201-4-5.

PSEUDOCYPRIDINA INORNATA (Peck)
Plate 48, figures 8–11

Cypridea inornata PECK, 1941, Jour. Paleontology, vol. 15, p. 301, pl. 44, figs. 33–36.

A fairly large, smooth, somewhat characterless species that is closely related to *P. piedmonti* Roth. The carapace of *P. inornata* is perfectly smooth and the posterior, dorsal, and anterior margins merge to produce a sweeping semicircle with only a slight angulation at the anterocardinal margin.

Distribution.—Lower Cretaceous. Kootenai at locality 23; Minnewaste limestone at locality 29; Lakota formation at locality 30.

Types.—Univ. Missouri, holotype 0-977-4; paratypes 0-977-3; figured specimens 0-1200-3-5.

PSEUDOCYPRIDINA LAEVICULA Peck, n. sp.
Plate 48, figures 1–4

Medium size carapaces, averaging about 1 mm. in length, subovate and rounded in lateral outline, highest at the anterocardinal angle, slightly depressed on dorsal side just posterior to anterocardinal angle, surface smooth, glossy. Anterior and posterior margins broadly and evenly rounded, ventral margin straight, dorsal margin sloping to the posterior. Beak small and inconspicuous or absent. Single rows of small papillae parallel the anterior and posterior margins on most specimens.

Remarks.—*P. laevicula* differs from *P. inornata* in shape, in possession of the small papillae paralleling the borders of most specimens, in the development of shallow, inconspicuous sulci, and in the greatly reduced beak and notch.

P. laevicula closely resembles *P.* (*Langtonia*) *dolabrata* Anderson in all characters except the development of papilla and sulci.

Distribution.—Common in the Bear River formation at localities 37, 38, and 38a.

Types.—Univ. Missouri, holotype 0-1200-1; paratypes 0-1084-2-4.

Genus ULWELLIA Anderson, 1939

Genotype: Ulwellia menevensis Anderson, 1939.

Cyprideinae with the right valve the larger and overlapping the left valve.

The genus *Ulwellia*, characterized by a reversal of valve overlap, is represented by several species in the European Jurassic and Cretaceous strata (Martin, 1940), but this is the first record of its presence in North America.

ULWELLIA MINUTA Peck, n. sp.
Plate 49, figures 9–11

Carapace small, averaging about 0.8 mm. in length, subquadrate in lateral outline, with a high, prominent anterocardinal angle. Beak and notch moderately well developed. Overlap moderate. Valves slightly depressed just posterior to anterocardinal angle along dorsal half. Surface covered with small pits.

Remarks.—This is the first species of *Ulwellia* to be described from North America. The known specimens number about 50 and are all small. Several species of *Ulwellia* have been described from Europe (Martin, 1940).

Distribution.—Lower Cretaceous. Confined to the Minnewaste limestone and associated shales at localities 28 and 29.

Types.—Univ. Missouri, holotype 0-1202-2; paratypes 0-1202-3.

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JOURNAL OF PALEONTOLOGY, VOL. 25, NO. 3, PP. 321–326, PL. 51, 3 TEXT FIGS., MAY 1951

INSTARS AND SHELL MORPHOLOGY OF *EOLEPERDITIA FABULITES*

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ABSTRACT—At least eight instars are recognized in *Eoleperditia fabulites*, ranging in length from 1.32 mm. to 11.43 mm. Secondary muscle scars are interpreted as representing the antennule, antenna, mandible, and perhaps the endoskeleton. The molting habit was well established in the Ordovician and differed little if any from the present process.

INTRODUCTION

THE leperditiid ostracodes have long been known as one of the oldest and most important families of bivalved crustaceans. However, only recently (Swartz, 1949) have we known much about the significant features of internal shell structure.

Dr. J. S. Templeton, Geologist, Illinois Geological Survey, discovered numerous leperditiid ostracodes in Middle Ordovician sediments of northern Illinois while mapping the Oregon Quadrangle. He kindly loaned the specimens which form the basis of this paper.

INTERNAL SHELL FEATURES

Swartz (1949) has described in detail most of the features found in the interior of leperditiid shells. Many of these structures are splendidly preserved on the Illinois material.

Prongs.—The inner-marginal prongs near each end of the ventral margin of the right valve have been interpreted as valve-stops by Swartz for the smaller left valve. There are four to six prongs at each end of the right valve, usually one or two more in the anterior end than in the posterior. An examination of the instars reveals the inner-marginal prongs in specimens as small as 2,000 microns, or what is here interpreted as the second molt. In the second instar there are five prongs in each end of the single specimen examined. Their size is in the same proportion to the shells as the size of the prongs in the adult is to shell size. The valve-stops may have been developed in response to the unusually strong adductor muscle, a muscle that was many times larger than that known in any other ostracode.

Adductor Muscle.—The adductor muscle scar is unusually well preserved in several of the Illinois specimens (pl. 51). One of them is preserved in such a manner that the scar is white on a dark background and therefore can be photographed in detail.

Swartz (1949) has sketched in excellent detail the muscle scar pattern of specimens from the Lowville limestone. He estimates

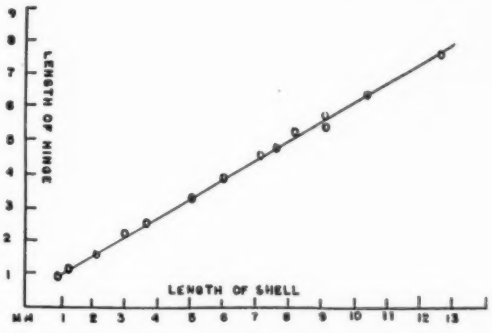


FIG. 1—Graph illustrating the relationship of shell growth to hinge length of *Eoleperditia fabulites*.

about 200 individual bosses within one scar. The scar pictured in the figures has approximately 190 bosses and a few are so small and indistinct that they may have escaped notice. The scar is posteroventral to the eye pit and slightly ovoid in outline. The individual bosses are irregular in outline and have minutely channeled and ribbed surfaces. Bosses in the posteroventral quadrant are smaller than the remainder. A comparison of muscle length, 4,800 microns,

to diameter, 2,000 microns, in an ostracode 10,200 microns long indicates an unusually strong closing muscle.

Another indication of strength is to note that muscle diameter equals two-sevenths the maximum height of the shell. Individual bosses within the adductor muscle scar attain a size of approximately 230 microns in diameter. This is larger than the entire muscle scar of most other ostracodes (Scott, 1944). The surface of each boss is sculptured with a pattern of minute ridges and grooves radiating from the center.

The adductor scar can be observed in many specimens from the exterior by coating the surface with oil or water. In some cases, where the scar has not been preserved on the inner surface, the details show remarkably well from the exterior. However, the venose lines ventral to the scar can be observed only from the interior on the Illinois specimens. The venose lines radiate from the ventral and anteroventral portion of the scar. They are strongly developed in the anteroventral area (pl. 51, fig. 2). These venose lines are interpreted as representing the contact of the chitin lining of epidermis with the inner surface of the calcareous layer.

Secondary scars.—Secondary muscle scars dorsal to the adductor were reported by Swartz (1949). He discussed their anatomical significance and suggested that they might function as mouth or appendage muscles, or muscles that worked the foregut or abdomen. These accessory scars can also be seen in several of the specimens from Illinois. They are seldom well preserved on the interior, and as observed by Swartz, can be seen best through the shell from the exterior. Anterodorsal to the eye there are two groups, scars a-a′; anteroventral and anterodorsal to the eye spot are groups of about ten muscle bosses, muscles b-b′. Dorsal to the eye and near the hinge two groups of about 20, muscles c-c′; posterior to the latter and along the hinge, a large group that might possess 50 or more bosses, muscle d; and dorsal to the adductor scar and posterior to the eye spot is a larger group of at least 20, muscle e; and scar f posterodorsal to the adductor (pl. 51, fig. 4). The number of bosses in the accessory muscle group varies between specimens probably because of preservation. Because of the rarity of the accessory muscle scars on the inner surface an attempt has been made to photograph them for the record (pl. 51, figs. 1–3, 5). An attempt was also made to photograph the scars from the exterior when the shell was submerged in mineral oil (pl. 51, fig. 4).

Swartz (1949, pl. 66, fig. 4) shows the secondary scars clustered in groups. This is probably a more accurately preserved set than those represented in the Illinois material, at least the clusters anterodorsal to the eye. The number of bosses in a secondary scar and the grouping shown by Swartz differs in detail from that illustrated in this paper. The reason for the variation is believed to be one of preservation. Only under the most fortunate circumstances should we expect these minute secondary scars to be preserved to the same degree of perfection.

TABLE 1—SIZE OF ADDUCTOR MUSCLE SCARS IN INSTARS OF *E. fabulites*

Instar	Length of shell (microns)	Diameter of adductor muscle (microns)	
		Dorsal to venter maximum	Anterior to posterior minimum
I	1,500	250	180
II	—	—	—
III	3,500	600	400
IV	4,900	1,000	700
V	7,200	1,600	1,200
VI	8,000	1,700	1,400
VII	10,500	2,000	1,600
VIII	12,000	2,500	2,000

Accessory muscles a–f performed functions other than closing the valves. Kesling (Univ. Ill. thesis, 1949, text-figures 5 and 5a) has made a detailed study of the musculature in *Cypridopsis*. On the basis of this study a reasonable interpretation of the accessory muscles in *Eoleperditia fabulites* is as follows: scars a-a′, dorsal and ventral rim muscles of antennule: scars b-b′, dorsal and ventral rim muscles of antennae: scars c-c′, mandible muscles; scar d, endoskeleton? muscles; e and f unknown, possible abdominal muscles. In *Cypridopsis* the muscles are attached closer to the hinge and more in a linear line than in *Eoleperditia*. The above interpretation connects the anterior muscle to the antennule, the second to the antenna, the third to the mandible, and the most posterior muscle to the endoskeleton. The accessory muscle scars are so situated that muscles a–c must pass anterior of the large adductor muscle; therefore, it is probable that they operated the three anterior appendages. The muscles attached to scars d-e could have passed either anterior or posterior to the adductor, but probably passed posterior and for this reason are assigned to the endoskeleton. This is a questionable assignment. In *Cypridopsis* the muscles operating the maxillae and the first and second legs are attached to the endoskeleton which in turn is attached to the shell in the dorsal area. For this reason none of the scars in *Eoleperditia* are ascribed to the posterior appendages. The position of the scars dorsal and anterior to the large adductor make it unlikely that any of these muscles could have been attached to the stomach. No evidence of furcal muscles was found in the posterior dorsal area.

The shell.—The shell is composed of closely packed columns of calcite with the "C" axis at right angles to the surface. In the first instar the shell is 50 microns thick, in the third 100 microns, and in the adult about 300 microns. Measurements were made in the medial posterior portion of the shell.

In some specimens a thin dark line appears externally and internally giving the shell a three layered appearance. The dark lines are only occasionally present and then may appear on only a portion of the shell. They are interpreted as remnants of the inner and outer chitin layers.

The hinge.—Hinge details are exceedingly difficult to recognize in the best specimens. Swartz described the right valve as nondenticulate but having a very faint groove. An examination of the interior of several good specimens indicates that the hinge of the right valve has a longitudinal groove in the posterior third of some individuals from the fourth instar to the adult (See pl. 51). It starts near the posterior cardinal corner and extends anteriorly one-third of the hinge length. In a specimen with a hinge 13,000 microns long the groove length is 4,500 microns; in a hinge 6,000 microns long the groove length is 2,300 microns. However, all specimens do not show the groove and I can find no counterpart of it in the left valve. Its significance is not clear. Teeth were not observed.

The hinge increases in length in direct proportion to the increase in the length of the shell. The cardinal ends of the hinge are represented by broad shallow concave to flat areas.

INSTARS

A sequence of shells ranging from 1,150 microns to 13,250 microns in length were studied and their measurements plotted on figure 2. This involved a total of 141 shells. The height-length ratios of all individuals do not fall in groups that show striking breaks between instars. The division lines between instars must be chosen somewhat arbitrarily. Two criteria have been used in choosing the boundary lines; first, consideration was given to any natural breaks which appeared on the graph, and second, the means of the early instars tend to fall closer together than the means of the late instars. However, Kesling (op. cit.) has shown that the means of the instars do not increase in direct ratio from the first to the last.

Fairly good natural breaks between instars are indicated on graph 2. However, with a larger number of measurements plotted it is likely that these gaps would tend to close, if not completely disappear. There can be no assurance that the boundary line between instars is accurately drawn. Only eight instars are indicated even

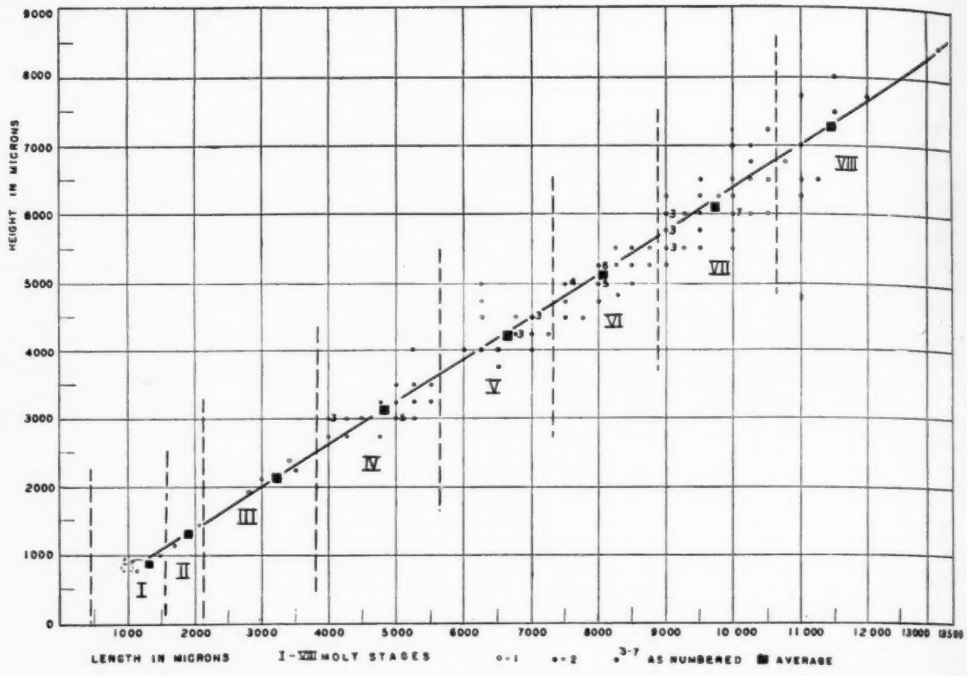


FIG. 2—Graph showing the range in size of the instars of *Eoleperditia fabulites*.

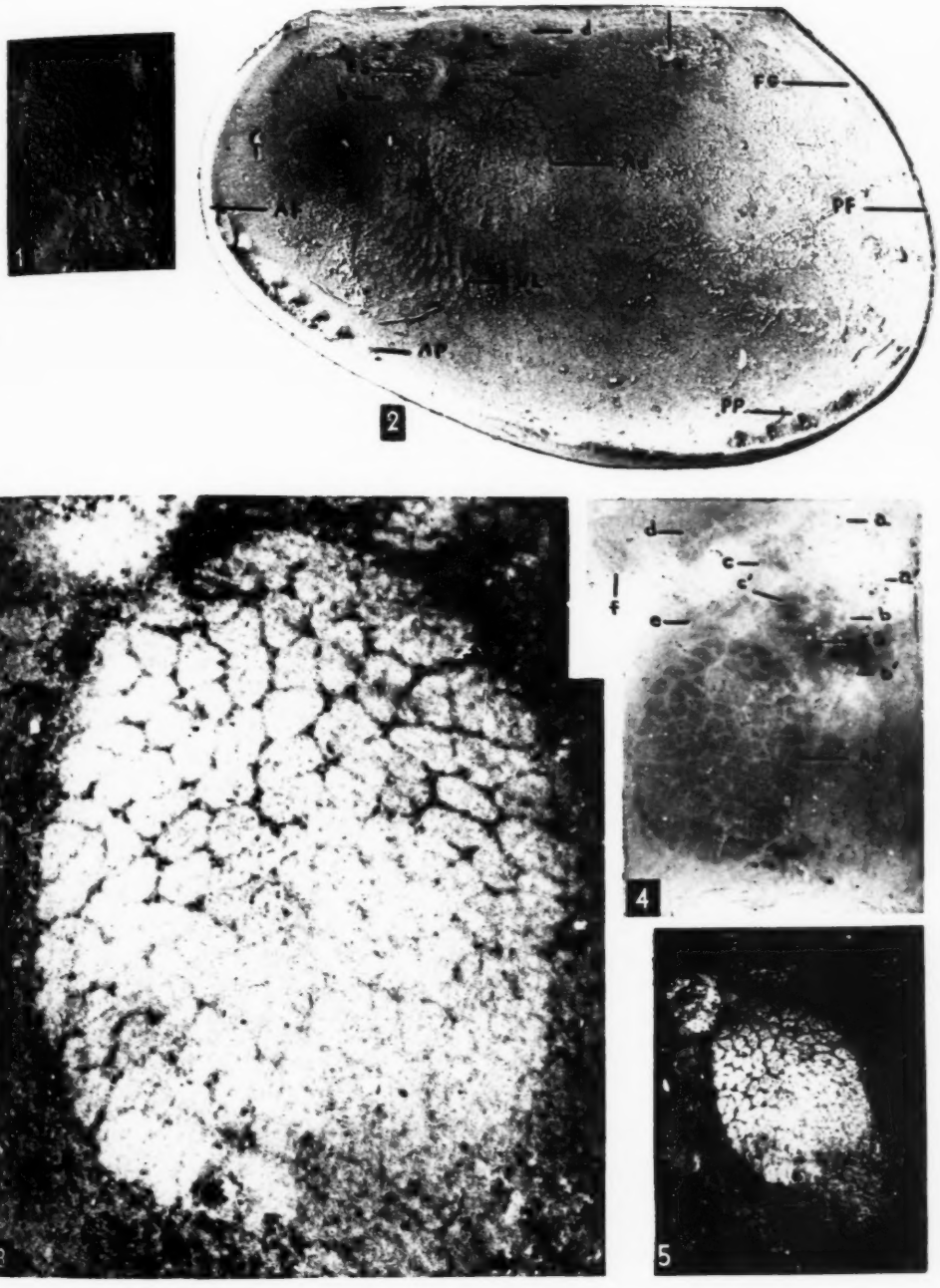
though nine may have existed. Swartz reports individuals up to 15,000 microns in length and 10,000 in height, and finds representative specimens to be 13,000 by 8,500 microns. This may indicate that the boundary between the eighth and ninth instars should fall on figure 2 at about the 12,500 micron line.

Instar I.—The shell is thin, about one-fourth or less than the thickness of the adult. The ends are subequally rounded and the long axis of the shell is approximately parallel to the hinge. A very faint depression on the interior represents the eye spot. The adductor muscle scar can be observed in one specimen, but it is too weak to show details. Prongs could not be observed. The height-length ratio could not be determined accurately with only two specimens.

Instar II.—In the second instar prongs are as well developed in comparison to the size of the shell as they are in the adult. One right valve shows four anterior and six posterior groups. The ends of the shell are still somewhat equally rounded and the long axis is approximately parallel to the

EXPLANATION OF PLATE 51

FIGS. *1–5*—*Eoleperditia fabulites* (Conrad). *1*—Interior of left valve, adductor muscle scar and eye spot, fifth instar, ×11, *2*—Interior of right valve of adult. Ad., adductor scar; b, antenna scar; c, mandible scar; d, e, endoskeleton? scars; LG longitudinal hinge groove; FG, flange groove; PF, posterior flange; AF, anterior flange; AP, anterior prongs; PP, posterior prongs; VL, venose lines; ES, eye spot. *3*—Adductor muscle scar of adult in figure *2*, ×37 Note radiate pattern on surface of individual bosses. *4*—Muscle scars on interior of right valve photographed through shell from exterior. Surface coated with mineral oil. Adult specimen, ×11. ES, eye spot; Ad., adductor scar; a, a′, antennule scars; b, b′, antenna scars; c, c′, mandible scars; e, d, endoskeleton? scars; f, unknown muscle scar. *5*—Adductor muscle scar of adult in figure *4*, ×10. Note eye spot and secondary scars dorsal to the adductor.



Scott, *Eoleperditia fabulites* shell morphology

hinge. The eye spot is a more pronounced interior pit.

Instars III and IV.—Very little change in general shape takes place in these instars.

Instars V and VI.—Ends of the shell become more pointed and the long axis appears more oblique to the hinge then in the first four instars.

Instar VII.—The length is greater in relationship to height than in any other instar; perhaps due to the first appearance of rudimentary sex structures.

Instar VIII.—This is here considered to be the sexually mature adult with ovaries and genitalia completely developed. The shell has an average length of 11.43 mm. and an average height of 7.26 mm. It is recognized that those attaining lengths of more than 13 mm. may represent a ninth instar, but the evidence is inconclusive because of the small numbers attaining that size in the Illinois material.

Reproduction.—Reproduction in *Eoleperditia* is thought to have been parthenogenetic. There is nothing in the shell morphology which would suggest the presence of males.

Ecology.—Most modern ostracodes are vegetarians, algae and diatoms forming the basis of their food supply. Kesling (op. cit.) found that altering the diet of *Cypridopsis vidua* to meat caused the colony to die out. However, Wohlgemuth (1914) successfully changed the diet of 20 of 21 species which he raised in cultures. There is no reason to believe that *Eoleperditia* was a scavenger. It is likely that the genus was also a vegetarian, feeding on diatoms and green algae. The green algae (chlorophydeae) live mostly in warm water in a well lighted habitat ranging from the tidal zone to a depth of approximately 60 feet.

The exceptionally strong appendage muscles of *Eoleperditia* suggests an animal that was a very capable swimmer.

Templeton* reports *Eoleperditia* to be abundant in the Mifflin, upper Magnolia, and Quimby's Mill members of the Platteville formation in northern Illinois. He divides the Quimby's Mill into two zones, an upper fucoidal, thick-bedded dolomite containing SiO_2 and abundant ostracodes, and a lower thin-bedded limestone in which fucoids and ostracodes are rare. In the upper Magnolia a massive cherty dolomite contains abundant ostracodes and fucoids. This relationship of ostracodes and fucoids is not accidental. If we interpret the fucoids as evidence of marine plants then we have a natural biotic relationship. The Mifflin member contains abundant ostracodes but only an occasional fucoid. However, the Mifflin is very argillaceous and contains numerous shale partings. The ostracode valves are orientated with their convex surfaces up. Other fossils, primarily brachiopods, bryozoa and trilobites, show evidence of wave action in broken shells and orientation. Wave action probably destroyed most plants that fell to the Mifflin sea floor and prevented development of fucoids, whereas the more rigid ostracode shells were preserved.

The little evidence available indicates that *Eoleperditia* was a free swimming animal living in warm water from the surface

TABLE 2—THE MEAN HEIGHT AND LENGTH OF THE INSTARS OF *Eoleperditia fabulites*

Instars	Mean Height Microns	Mean Length Microns	No. of Specimens Measured
I	880	1,325	2
II	1,900	1,300	4
III	2,150	3,175	6
IV	3,145	4,795	25
V	4,247	6,638	20
VI	5,116	8,039	29
VII	6,063	9,773	43
VIII	7,263	11,435	11

* Personal communication.

down to a depth not greater than that in which algae lived. The shells at death, or during molting, fell to the sea floor and accumulated in the bottom sediments. The primary factors controlling distribution were food supply (algae and diatoms), temperature, and light.

Photography.—It is not always possible to find open valves with internal features well enough preserved to be photographed. On the other hand, specimens that appear opaque from the exterior may show internal features when the shell is coated with a liquid. It seemed possible to photograph these internal structures through the shell by coating the surface with mineral oil and adjusting lights at a low angle. The results of this method are illustrated in plate 51, figure 4.

Location.—All figured specimens come from the Mifflin member, Platteville formation, quarry Medusa Cement Plant, sec. 27, T. 22 N., R. 9 E., Lee County, Illinois. Other material studied came from: SE ¼, NW ¼, SW ¼, sec. 23, T. 1 N., R. 6 E., Green County, Wisconsin (Quimby's Mill); SW ¼, NW ¼, sec. 22, T. 22 N., R. 9 E., Lee County, Illinois (Mifflin).

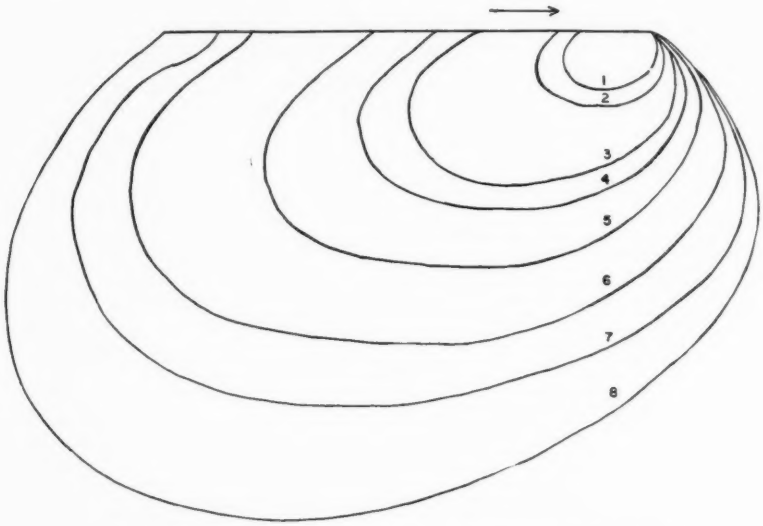


FIG. 3—Camera-lucida outlines of the instars of *E. fabulites*.

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JOURNAL OF PALEONTOLOGY, VOL. 25, NO. 3, PP. 327–335, PL. 52, 3 TEXT FIGS., MAY 1951

MOLT STAGES OF AN EOCENE FRESH-WATER OSTRACODE

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ABSTRACT—Fresh-water ostracodes pass through nine instars, the last representing the sexually mature individual. All instar stages of fossils can be recognized in *Candona whitei*, n. sp. Three hundred and ninety-two specimens ranging from the egg to the mature adult have been measured. The height-length ratio varies considerably between individuals of the same species. The mean height-length ratio is the same for most instars but exceptions exist. The process of molting bears directly upon ostracode taxonomy and phylogeny.

INTRODUCTION

THE process of molting in both modern and fossil ostracodes has been known, in a general way, for a long period of time. However, very little detailed work has been done on the molt stages of either fossil or living species. Betty Kellett (1943), Cooper (1945), Roy (1939) and Hessland (1949) have recognized molt stages in fossil marine ostracodes but no reports of molting in fresh-water forms have been made.

A study of the Ostracoda during the past few years has convinced the senior writer that molting and the problems connected with it are fundamental in the classification and interpretation of ostracodes of all ages. Such problems as orientation, height-length ratio, family and generic relationships, and many features of a structural nature can be best understood when an entire suite of molts has been studied. Literature, primarily the old, is filled with too many species which have been described as new, and too many references have been made to the structural features of ostracode shells based upon data which could more properly be attributed to changes inherent in the molting process of these complex crustaceans. Considerable reliance has been placed by many upon the height-length ratio without any evidence to support the general contention that such a ratio is constant.

This study was undertaken to determine what changes could be found in the shells of a single species of fossil ostracode. For that purpose a species was chosen in which numerous individuals were readily available. Such an ostracode is *Candona whitei*, n. sp. from Eocene shales of southwestern Wyoming. This species occurs in such abundance that it forms coquina-like beds of limestone in the Bridger and Green River basins. Due to the abundance and the almost perfect preservation of the material it forms an ideal basis for the study of molting in fossil fresh-water ostracodes.

Acknowledgement is hereby made to the aid of Harold R. White, The Pure Oil Co., New Orleans, La., who made a preliminary study of this species for a master's thesis at the University of Illinois in 1947.

STRATIGRAPHY

All of the material used in this study was collected from two localities in the southwestern part of Bridger Basin, Wyoming. The collecting localities are in Uinta County in the southwestern part of section 11, T. 15 N, R. 117 W. and section 6, T. 15 N., R. 116 W., along U. S. Highway 30-S, approximately 10 miles west of Fort Bridger, Wyoming.

The samples were collected from the Green River formation of middle Eocene age. The collecting zone is near the top of the Green River formation as exposed on the west side of the basin. In this area the formation is composed of sands and shales with thin limestones and thinly laminated calcareous shales. The calcium carbonate content increases toward the top. The clastic material increases downward so that the boundary line between the sands and shales at the top of the Knight and the base of the Green River is difficult to determine.

The number of ostracodes, in general, varies as to the amount of calcium carbonate in the sediments. An exception to this is the occurrence of thin, hard, brittle limestones that contain only a few ostracodes. In this portion of the basin the Green River formation does not contain an abundance of oil shales, and appears to be a different facies than sediments of the same age on the east side of the basin.

METHODS OF STUDY

In the recovery of specimens, screens ranging from 20 mesh to 200 mesh were used. The small screen sizes are necessary for the recovery of the early molt stages. Many of the more important specimens may be lost if the small screen sizes are not used. It has been customary, in the study of ostracodes, to collect only those which remain in the 40, 60, and 80 mesh screens. This is inadequate for a study of ostracode instars.

Most of the ostracodes can be removed by partial crushing and then washing after a period of stewing in a solution of sodium hydroxide. Samples that contain large quantities of calcium carbonate can be broken down only by mechanical methods. Both methods were used and numerous complete specimens of variable sizes were obtained.

A total of 392 specimens were measured and the results plotted on graph paper. The maximum height and length (commonly used as the basis of the height-length ratio) was measured with a micrometer scale in the ocular of a binocular microscope.

MOLTING IN MODERN FRESH WATER OSTRACODES

Very little work has been done in America on the ontogeny of fossil or living ostracodes. The most significant work in this country is that of Kesling (Univ. Illinois thesis, 1949) on *Cypridopsis vidua*. European investigators have been active in the study of the life history of living species, but even there little has been done on fossil species.

It is known that in the fresh-water species nine instars occur. There may be slight differences in the development of species, but in general the egg hatches into a nauplius with three pairs of appendages and inclosed in a bivalved shell. These appendages represent the antennules, antennae and mandibles. In a general way an additional pair of appendages or a modification of the appendages appears in each of the first seven molt stages.

Claus (1872) studied the instar stages of *Cypris ovum* (Jurine) and *C. fasciata* (Müller), Schreiber (1922) has studied *Cyprinotus incongruens* (Ramdohr) and Kesling (op. cit.) worked out the larvae stages of *Cypridopsis vidua* (Müller). The relationship of the appearance of appendages to instar stages as worked out by Müller and Kesling follows:

Instar	No. of Appendages	*Cypridopsis vidua*
1	3	(antennule, antenna, mandible)
2	3	(with incomplete maxilla and furca)
3	4	(furca incomplete)
4	4	(furca and 1st thoracic leg incomplete)
5	5	(2nd thoracic leg incomplete)
6	6	(3rd thoracic leg incomplete)
7	7	(ovaries incomplete)
8	7	(ovaries, genitalia incomplete)
9	7	(ovaries and genitalia)

This sequence is believed to be true for all Cypridae and is probably true for most ostracodes. The order of development is significant in the study of fossils because the shape of the shell may change during the various instars. Thin shells without posterior inflation could represent one of the first seven instar stages prior to the development of the ovaries or they might represent males. A study of such common genera as *Bairdia*, *Healdia*, *Bythocypris*, and *Cytherella* leads to the conclusion that numerous new species have been erected on early molt stages.

MOLTING IN *Candona whitei*

The height-length ratio of 392 specimens is plotted on figure 1. The boundary line between molt stages is obvious in some instances. Natural breaks occur between all molt stages except VII and VIII. This boundary line was chosen at approximately

the midpoint between the breaks at the base of VII and IX. In other species with which we are working at the present time we find that breaks between molt stages may be less apparent than they are in the case at hand.

It may be noted that a great variation exists between the number of specimens occurring in each molt stage. This variation is not completely understood. Theoretically, the largest number of specimens should exist in the first molt stage; actually this is where the smallest number are found as fossils. The largest number of fossils is found in the V, VI, and VIII instars. The small number of individuals in stages I and II can probably be accounted for by the fragile nature of the early shells. Observation of the shells in the early stages of modern fresh-water ostracodes indicates that the amount of calcium carbonate present is less than it is in the later molts; no quantitative measurements have been made. The young shells are usually thinner and more flexible than in the older stages. The few specimens which have been recovered from the earliest molt stages have been bivalved shells; for that matter, a single valve in the material under study is exceedingly rare. This may mean that the valves of this species remained joined along the hinge after molting was completed; that is, the animal removed itself from the old shell without the valves ever having been disjoined. This is not true in all cases of ostracode molting.

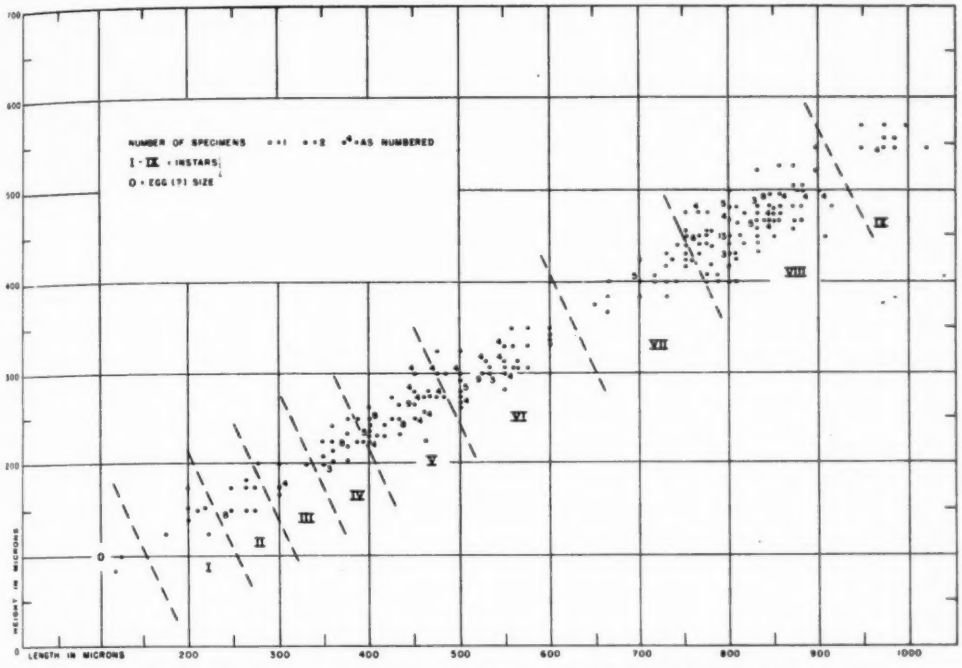


FIG. *1*—Height-length ratio in 392 specimens of *Candona whitei* Scott & Smith, n. sp.

The number of fossils should vary in inverse ratio to the age of the instars. In most studies of ostracodes only the adults have been recovered or described. Therefore, we have very little data concerning the abundance of individuals in various molt stages. From our study of *C. whitei* and from observations of many samples of both marine and fresh water material, we are under the impression that the late molts and adults are more numerous than those of the early stages.

On figure 2 we have plotted the average of the height-length for each instar. A

straight line has been drawn so that it passed through the mean point of the greatest number of instars. This represents the normal growth line, assuming a constant height-length ratio. It will be noted that the growth line passes through the mean of all molt stages with the exceptions of I and VI. The mean of instar I falls above the line, that is, in this instar the height is greater in proportion to the length than in any other stage of molting because there has been only a slight modification from the spherical egg. Even though only nine specimens were recovered from instar I, it is believed that the mean as shown is indicative of this molt in most ostracodes. The first molt has changed only slightly from the spherical egg and therefore we would expect the height to be greater in proportion to the length than in any other instar.

The mean of instar VI falls below the growth line. This may be due to some biological reason that is not now apparent. If the furca was completed at this point it might cause a sudden increase in the length of the carapace without a corresponding change in height. The latter explanation seems the most logical but information is not available to prove the point conclusively. If most species of the genus should show a similar anomaly, then it could probably be ascribed to completion of the furca.

The appearance of only 30 specimens in stage VII is the most disturbing anomaly in the data on *C. whitei*. In the process of our study two different sets of samples were run by different workers. Each investigator found the same condition present. It is obvious that the large number of individuals found in stage VIII had instar ancestors in stage VII. However, for some unknown reason the molts in instar VII were not preserved. This may mean that those shells which we find are of animals that met an accidental death and that due to the appearance of all appendages by instar VII the animal was more active. Only a small percent met death in an accidental fashion, whereas in stage VIII the death rate was higher. It is obvious from the records of stage IX that only a few became sexually mature animals. Only a few more specimens of adult size were found than in the smallest molts of instar I.

The slightly increased length of instar VII, probably due to the first appearance of sexual structures though sexual maturity, is not attained until instar IX.

FOSSIL OSTRACODE EGGS

While examining the samples for the smaller ostracode instars Harold White (1948) found in the 220 mesh screen two minute spherical bodies which may represent fossil ostracode eggs. On first thought this might seem like an impossible discovery but the evidence seems to support the suggestion.

Numerous eggs of *Cypridopsis vidua* were obtained by Kesling during his study of cultures of this modern species. These modern eggs were examined by the senior writer. They were approximately spherical in shape, with a narrow and shallow equatorial groove, and covered with small pits. At the time of hatching the egg breaks along the equatorial groove, splitting into two similar portions. The covering of the egg is composed of chitin and calcium carbonate. It is rigid and readily maintains its spherical shape. The shell appears to be as rigid as the shell of the early instars. There is no reason why these eggs cannot be preserved as readily as any other portion of an ostracode shell throughout its life history. We considered the possibility that these small spherical bodies might represent oolites. However, there were no oolites of larger size in any of the screens. The surface of the eggs is slightly pitted as though it might once have been the base of hair-like structures. However, the irregularities are so indefinite that they cannot be classified with certainty as true pits in an original shell. When the size of these spherical bodies is determined and plotted upon the graph of instar sizes they fall in the predicted position. Furthermore, they are the same size as the eggs of *C. vidua*, about 105 microns in diameter. As a check upon this interpretation two separate samples were run for the precise purpose of discovering additional eggs and in each case one spherical body was found. It must be borne in mind that they were found on only the 220 mesh screen and that only two specimens were recovered from a sample that yielded 400 or more ostracode shells.

Fossil ostracode eggs should be a common rather than a rare occurrence. The eggs of

modern species usually collect on plants or the floor of the pond or lake where they may remain undeveloped for several months, often surviving periods of drought and freezing temperatures. Sars (1901) often developed ostracode cultures from foreign lands by importing mud to Norway. The mud containing ostracode eggs was placed in the proper environment in aquaria where the ostracodes soon developed. It is apparent that such eggs with their calcareous shells must have abounded in the muds on the floors of ancient Eocene lakes in Wyoming. The evidence that the spherical bodies which we are describing represent eggs is not conclusive, but is strong enough to warrant calling them to the attention of other workers.

PARTHENOGENESIS OF *C. whitei*

Reproduction in fresh water ostracodes is known to vary in different species. Hoff (1942) has classified reproduction under four heads:

(1) Males unknown, reproduction parthenogenetic. Several genera and numerous species have been listed as reproducing in this manner. In the several hundred specimens of *C. whitei* which we have examined we have been unable to recognize a single specimen which might be classified as a male. We believe that the reproduction in this species was wholly parthenogenetic and that the life history was very similar, if not identical, to that of many species of modern *Candona*.

(2) Males occasionally found, reproduction usually parthenogenetic. Klie (1926) found that the number of males present in *Cyprinotus incongruens* was related to latitude; males rarely found in Germany but abundant in North Africa.

(3) Males rare, reproduction both syngamic and parthenogenetic. No evidence to support an alternation of reproductive methods in ostracodes has been found.

(4) Males always present, reproduction syngamic. By far the greater number of species falls within this classification.

HEIGHT-LENGTH RATIO

Considerable importance has been attached to the height-length measurements of ostracode shells. Kesling (op. cit.) has shown that considerable variation exists in this measurement within individuals of the *Cypridopsis vidua*. The measurements of 392 specimens of the Eocene *Candona whitei*, as plotted on figure 2, show that considerable variation may be expected to occur in the height-length ratio of fresh-water fossil ostracodes. Extremes in height between specimens of the same molt stage may vary as much as 100 microns. Extremes in length in individuals of the same molt stage may also vary as much as 100 microns. In fact, the boundary lines between molt stages of *C. whitei* as shown on figure 2 are approximately 100 microns apart. For example, if we relied upon one specimen for determining the height-length ratio, we could get such extremes as found in the fourth instar of *C. whitei:* one individual has a height-length ratio of .66, another individual has a ratio of .52. Obviously there is considerable range in the height-length ratio of individual ostracodes in the same species. We can conclude that the height-length ratio of a given specimen is somewhat worthless and cannot be used as a specific characteristic in the classification of ostracodes. This does not mean that the height-length ratio has no value because with an adequate number of specimens of the same species it is obvious that the mean height-length ratio can be determined, but even there we do not feel that it is by itself of great specific value in classification. The chief value is for the purpose of understanding the development of instars and to discover anomalies that may occur along the normal growth line.

CONSTRUCTION OF GROWTH-LINE DIAGRAMS

There are certain erroneous concepts in literature concerning the form and interpretation of curves showing the growth of an ostracode. The first of these is that the growth line is straight when passed through the mean of all molts, the second that the form-ratio of individuals of a given species is constant, and the third that a projection of a straight line passed through the mean of all molts will always pass through the "0" point.

Kesling has shown that the mean of all instars should not fall on a straight line. Kellett (1933) has shown that considerable change in shape occurs between the early molts and the adult. When the spherical

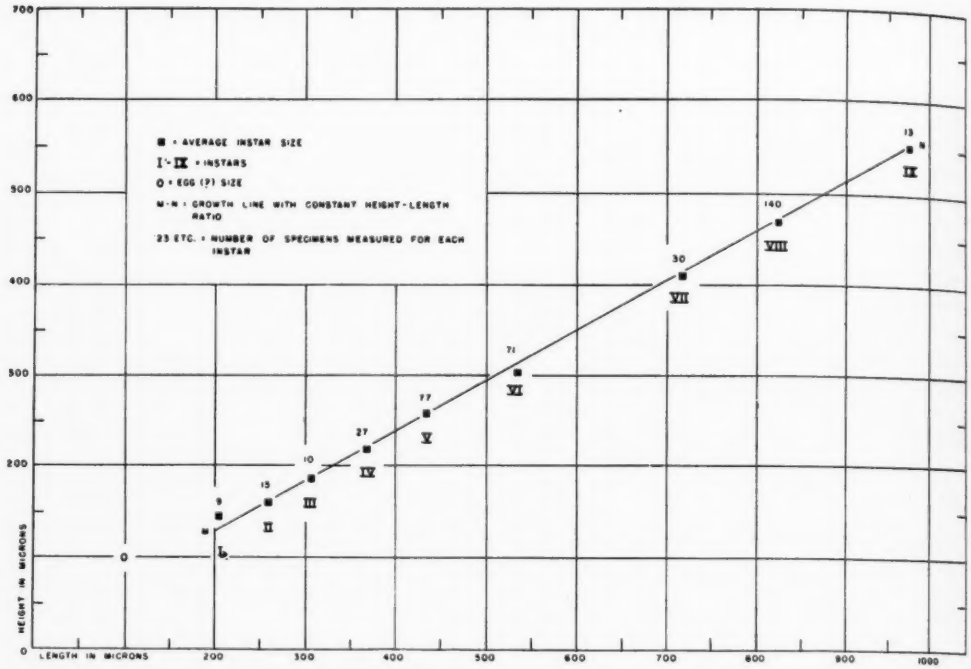


FIG. 2—Averages of height-length ratios in *Candona whitei* instars.

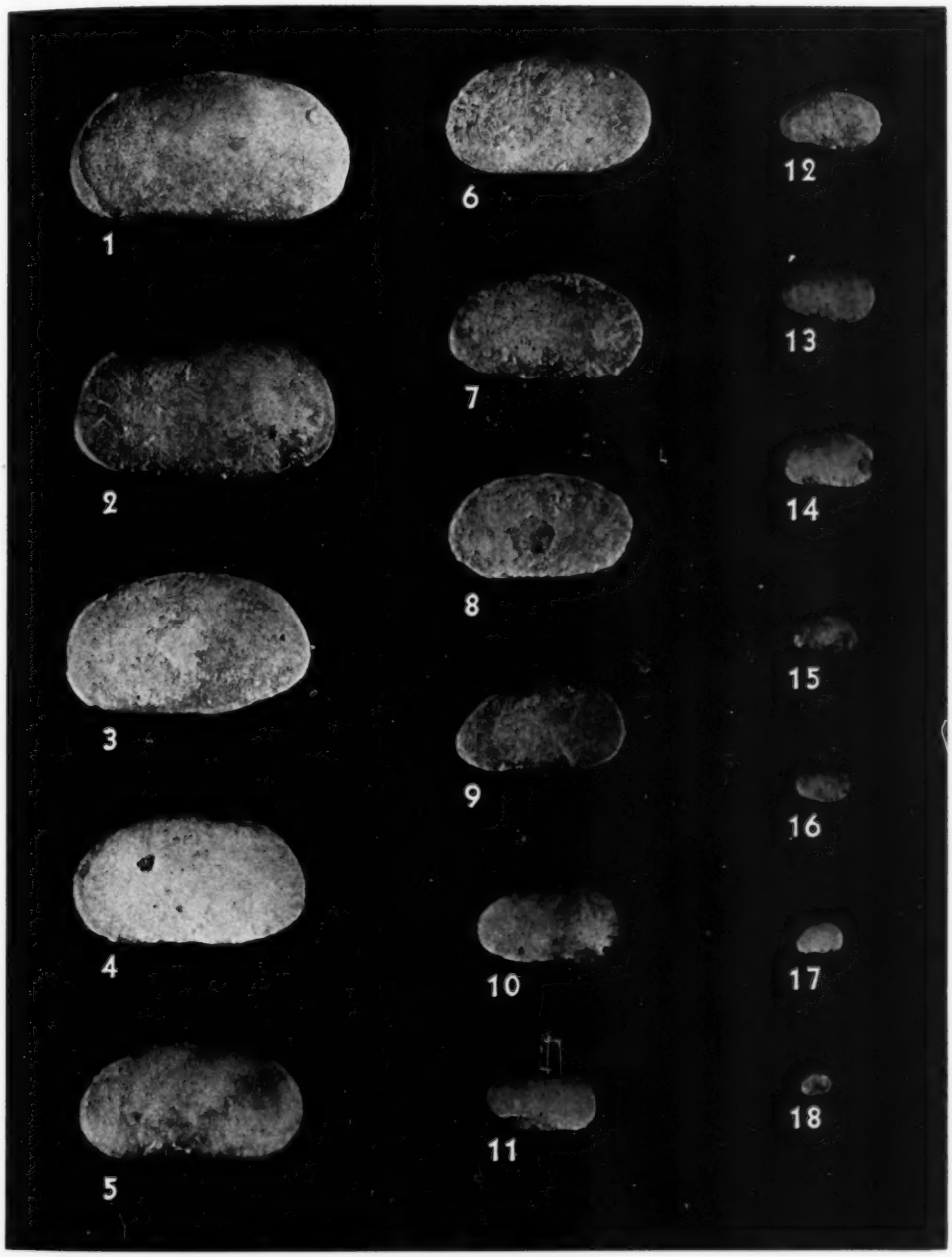
egg hatches into the naupalis only a slight deviation from sphericity is needed because the full complement of appendages and posterior body parts is not present. The mean of the first instar should fall above a straight line passed through the maximum number of means. Cooper (1945) drew a curve for *Ectodemites plummeri* through "median" points for each instar. We assume that "average" or "mean" was intended instead of median. The curve for *E. plummeri* was started at the "0" point and extended to the mean of the ninth instar. The fact that the line passed through at least six of the instar averages is probably accidental rather than indicative of ostracode molting in general. If a straight line had been drawn from the spherical egg of 100 microns diameter, or even 75 microns, to the mean of the adult stage it would have fallen above the mean of all of the first eight instars. Cooper (1946) recognized the importance of the molt stages in taxonomy and considered several "species" of *Sulcella* as molts of a single species. The same is true of *Carbonita* and it is almost certainly true that all fossil ostracode genera contain pseudo-species.

In considering the best method of drawing a growth-curve we studied three possible methods, (1) from "0" to the mean of the adult, (2) from the spherical egg (100 microns) to the mean of the adult, (3) a straight line passing through the mean of the greatest number of instars including the adult. Of these, the first method seemed the least accurate and the third seemed to show best the deviations from the normal.

EXPLANATION OF PLATE 52

All figures ×36, of left valves.

FIGS. *1–18*—*Candona whitei* Scott & Smith, n. sp. *1*, *2*, adults, IX instar; *3–5*, VIII instar; *6–8*, VII instar; *9*, *10*, VI instar; *11*, V instar; *12*, IV instar; *13*, *14*, III instar; *15*, II instar; *16*, *17*, I instar, *16* slightly flattened; *18*, egg?



Scott and Smith, Molt stages of *Candona whitei*

TABLE I

Measurements in microns of instars of C. whitei

I		II		III		IV		V		VI		VII		VIII			IX		
H	L	H	L	H	L	H	L	H	L	H	L	H	L	H	L	H	L	H	L
125	225	175	275	200	275	200	350(3)	250	387(2)	300	475(4)	408	716	475	816	500	896(4)	572	946
150	216(2)	150	275	200	300(2)	208	350(2)	232	400(5)	300	482	400	716	442	816	482	916	572	972
150	208	175	267(2)	175	300(4)	225	350(2)	225	400(4)	325	500	425	700	450	808	450	908	572	996
175	200	150	267	167	300	208	362(2)	242	400(2)	300	500(4)	400	700(5)	467	808(2)	508	882	560	972
150	200(2)	175	250	200	332(2)	216	362	250	400(8)	292	500(2)	400	667	482	808	500	882(5)	546	972(4)
142	200	150	250(8)			225	362(2)	267	400	282	500(5)	385	700(2)	432	808	482	882	546	946(2)
125	175	182	267			242	362	237	400	275	500(4)	382	667	425	808	467	882	560	985
						220	375(8)	232	408	267	500	367	667	500	800	500	875(3)	546	985
						208	375	232	432	260	500	375	650	482	800(8)	467	875	546	1020
						250	375	232	416	325	475	382	732	467	800(5)	525	872		
						232	375	225	460	300	525(9)	400	742(2)	450	800(3)	508	872		
						225	392	242	416	300	532(3)	400	732(2)	442	800	485	872		
						225	387(2)	250	432(8)	300	550(4)	416	732	432	800(3)	460	872		
								250	450(4)	285	550(2)	432	732(2)	416	800	525	860		
								250	425(2)	332	600(2)	425	750	400	800	496	860(4)		
								260	460(4)	337	600	425	757	400	787	485	860(2)		
								267	450(9)	342	600	425	742	416	787	475	860		
								267	432(2)	350	600	416	750(2)	460	782(2)	467	860		
								275	475(4)	308	550	432	750	436	782	482	850		
								275	460(4)	308	532	437	750	416	782	475	850(4)		
								275	425	308	560	442	742	475	775	467	850		
								275	467	308	567			460	775	450	850(2)		
								275	482	310	575(2)			450	775(2)	496	846(8)		
								282	450(4)	316	550(4)			442	775	485	846		
								300	450(4)	316	567(2)			410	775	467	846(4)		
								282	467	316	532(4)			400	775	467	842		
										326	550(4)			475	767(4)	522	832		
										326	575			450	767(6)	482	832(3)		
										326	560			442	767	475	832(2)		
										350	575			432	767(2)	467	832(5)		
										350	560			475	750	457	832		
														457	750	450	832		
														450	750	442	832		
														546	896	432	832		
														524	896				

( ) number of specimens of given size

SHAPE OF SHELL

From the approximate spherical shape of the egg the ostracode grows to become an elongate-ovate form. In instar I the shell has its greatest height in relationship to length. These changes of form are illustrated on figure 3. Individuals grading in size from the egg to the extreme of the adult were chosen for camera lucida outline drawings. These outline drawings were placed with their anterior ends adjacent and the growth picture of the various instars was thus developed. It shows a progressive and rather consistent increase in length. This is a

TABLE 2—RANGE OF INSTAR SIZES (MICRONS)

Instar	No Specimens	Range		Average	Height-Length Ratio
		Height	Length		
Egg	2	85–100	116– 125	92×120	
I	9	125–175	175– 225	146×204	.71
II	15	150–182	250– 275	159×258	.62
III	10	167–200	275– 332	187×304	.61
IV	27	200–250	350– 392	218×367	.59
V	77	225–300	387– 482	258×434	.59
VI	71	260–350	475– 600	306×532	.57
VII	30	367–442	667– 757	407×718	.57
VIII	140	400–546	750– 916	468×824	.55
IX	13	546–572	946–1020	554×974	.57

fairly good picture of the growth of an ostracode with a convex hinge line. The straight-backed ostracode may show a similar growth pattern.

SYSTEMATIC DESCRIPTION

Order OSTRACODA Latreille 1802
Family CYPRIDAE Zenker
Group SIMPSONATA n. gr.
Genus CANDONA Baird 1845
CANDONA WHITEI Scott & Smith, n.sp.
Plate 52, figures 1–18

Adult.—Shell subovate in lateral view, dorsum broadly convex, venter straight to slightly concave at midpoint; anterodorsal slope long and evenly convex; greatest extension of ends median to slightly submedian; greatest height slightly anterior of median; dorsal view elongate-ovate, greatest thickness in posterior half, slit-like gap between valves along line of hingement. Valves approximately equal, left slightly larger than right along ventral margin; surface appears smooth; muscle scars unknown.

First and Second Instars.—Ovate, anterior end broadly rounded, posterior end acuminate; greatest height anterior; shell thin.

Third and Fourth Instars.—Posterior end becomes more rounded, less acuminate than in first and second instars.

Fifth and Sixth Instars.—Posterior end still narrower than anterior, but only slightly acuminate.

Seventh through Ninth Instar.—Posterior end broadly rounded and similar to anterior end; acuminate form of posterior end in early instars completely missing.

Relationships.—The genus *Candona* contains a large number of living species. Most authors divide the genus into seven groups. These groups are distinguished on the basis of anatomical features, especially differences in the thoracic appendages, sexual lobes, or setae. These groups cannot possibly be recognized from the shells alone and, therefore, group names as applied to modern species of *Candona* cannot be used in the classification of fossil species. Insofar as shell shape is concerned there appears to be only two groups within *Candona;* one consisting of elongate-ovate shells with a smoothly convex dorsal margin similar to *C. simpsoni* Sharpe 1897, and a second group of shells in which the antero- and posterodorsal slopes are truncated, causing these edges to be somewhat straight and the margin along the hinge straight to gently convex as in *C. biangulata* Hoff 1942. *C. whitei* belongs to the *Simpsonata* group. It is here proposed to classify the fossil shells into two groups as indicated above, the *Simpsonata* and *Biangulata* groups.

Ecology.—Members of the genus *Candona* live under a variety of fresh water environmental conditions. The majority of them inhabit water in which there is no current or only slight current. *C. simpsoni* is a com-

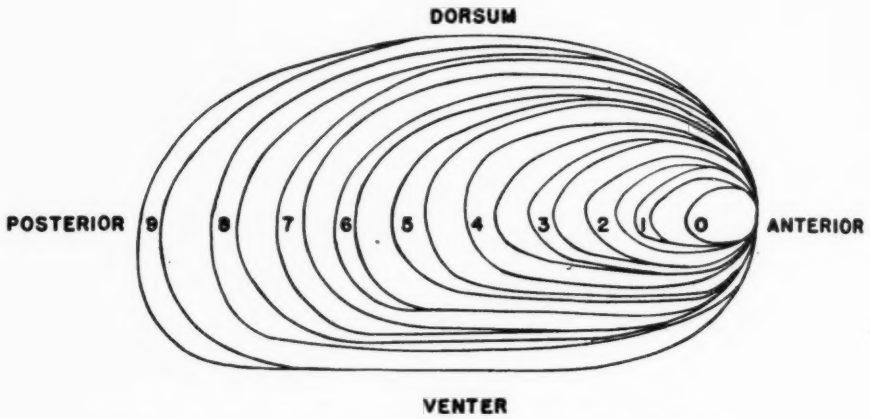


FIG. 3—Outlines of instars of *Candona whitei* Scott & Smith.

mon bottom dweller of lakes and ponds, occasionally found along the shores of rivers. Hoff (1942) reports that most of his collections of this species were obtained from "masses of algae along the edge of ponds and sluggish streams." Other species of this type have been collected from permanent lakes. They were found most commonly associated with grass, algae, decayed vegetation, and aquatic vegetation (spermatophytes).

Occurrence.—All specimens studied come from the upper portion of the Green River formation in the southwestern portion of Green River Basin, Wyoming.

Types.—Holotype—University of Illinois X-1456; paratypes—1456a–q.

MANUSCRIPT RECEIVED MAY 22, 1950.

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STUDIES ON CARBONIFEROUS INSECTS FROM COMMENTRY, FRANCE: PART II. THE MEGASECOPTERA

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ABSTRACT—This is the second in the series of papers redescribing the Carboniferous insects of the Commentry Basin, France. It deals with members of the Order Megasecoptera, and contains an account of the wing and body structure of all species unquestionably belonging to the order. Two new families, Sphecopteridae and Ischnoptilidae, are established as a result of reclassification of the fossils.

INTRODUCTION

BRONGNIART established the "Family" Megasecopterida in 1885 for four genera of insects in the Commentry shales. He originally assigned the group to the Order Pseudoneuroptera, along with the Odonata and Ephemerida, but following Scudder's classification of Paleozoic insects, he later (1894) transferred it to the "neuropteroid" series of the Order Palaeodictyoptera. Handlirsch subsequently (1906) elevated the group to an order, which he termed Megasecoptera, and included within it several insects from other Carboniferous deposits. Since then, many additional Megasecoptera have been described from Permian as well as Carboniferous strata, the order now including 17 families and 35 genera. The Commentry specimens, however, are still the most important Carboniferous representatives of the order. This is in part due to their excellent preservation, and in part to the diversity of the Commentry fauna. Of the ten families and 15 genera of Carboniferous Megasecoptera known, six families and 11 genera contain Commentry species exclusively. Unfortunately, however, largely as a result of the compilatory nature of Handlirsch's work and the superficiality of Meunier's, the published accounts of the Commentry Megasecoptera are unsatisfactory. The purpose of the present paper, which is based upon a study of all known Commentry material, is the redescription of these fossils, with a revision of their family, generic and specific assignments. The family Diaphanopteridae, although apparently megasecopterous, is not included here; it is so far removed from the other Commentry families that a separate account of the fossils and their affinities seems advisable.

SURVEY OF COMMENTRY SPECIES

A historical account of the Commentry collections and of the general literature on the fossils was included in the first of this series of papers (Carpenter, 1943). Previous work on the Megasecoptera has been done by Brongniart, Meunier, Lameere and Handlirsch, and discussions of their accounts have been published by Martynov, Forbes and Carpenter. The fourteen species treated in this paper have previously been placed in four families (Aspidothoracidae, Mischopteridae, Corydaloididae and Foriidae), but I have found it advisable to add two new families (Sphecopteridae and Ischnoptilidae) because of peculiarities which I consider of more than generic value. The following is the classification proposed here:

Family ASPIDOTHORACIDAE
  Genus *Aspidothorax* Brongniart
    triangularis Brongniart (synonyms: *maculatus* Brongniart, *nanus* Handlirsch)
Family MISCHOPTERIDAE
  Genus *Mischoptera* Brongniart
    nigra Brongniart (synonyms: *woodwardi* Brongniart, *concolor* Handlirsch, *ocellata* Handlirsch, *infumata* Handlirsch)
  Genus *Psilothorax* Brongniart
    longicauda Brongniart (synonym: *pictus* Handlirsch)
Family SPHECOPTERIDAE (new)
  Genus *Sphecoptera* Brongniart
    gracilis Brongniart
    brongniarti Meunier
    minor Brongniart
    elegantissima Meunier
  Genus *Cyclocelis* Brongniart
    chatini Brongniart (synonyms: *brongniartiana* Handlirsch, *fenestrata* Handlirsch)
    obscura Brongniart
  Genus indet.
    acuta Brongniart

Family ISCHNOPTILIDAE (new)
Genus *Ischnoptilus* Brongniart
elegans Brongniart
Family CORYDALOIDIDAE
Genus *Corydaloides* Brongniart (synonym: *Corydaliodes* Handlirsch)
scudderi Brongniart (synonyms: *brongniarti* Handlirsch, *longipennis* Handlirsch, *simplex* Brongniart, *gracilior* Handlirsch)
Family FORIRIIDAE
Genus *Foriria* Meunier
maculata Meunier
Insecta Incertae Sedis
pulchra Brongniart (Sphecoptera)

All of these species belong to that series of Megasecoptera which were strictly palaeopterous, i.e., unable to fold their wings over the abdomen at rest. I have previously discussed the composition of this series in my account of some Megasecoptera from the Permian of Oklahoma (Carpenter, 1947). The palaeopterous nature of these insects is not inferred from the venational pattern but is indicated by the position in which the wings are preserved in the fossils. Neopterous insects, as a general rule, die with the wings held in the resting position, over or along the abdomen; whereas the palaeopterous types die with the wings outspread. All of the specimens of Megasecoptera treated in this paper are preserved with their wings outspread, which is especially significant in the cases where there are several fossils of one species. Although no member of this particular series of Megasecoptera is entirely generalized in its characteristics, the Aspidothoracidae seem to have more such features than any other family, e.g., the nearly even distribution of cross-veins over the wing, the independent origins of main veins and the complete absence of anastomosis of veins. On the other hand, the crowding of Sc, R1, and the basal stems of M and Cu along the anterior margin is a specialization which, although appearing in some other members (such as the Permian Bardohymenidae and Protohymenidae), is absent in other Commentry families. Within this series of Commentry species, also, there is a tendency for wing petiolation, which reaches its maximum development in the Sphecopteridae. The occurrence of wing maculations in some of the Commentry species is especially noteworthy (see plate 53, figure 2), such markings being unknown in Permian Megasecoptera.

The body structure of the Commentry Megasecoptera is very incompletely known. Handlirsch's reconstructions of *Mischoptera* and *Corydaloides*, which were published in Schröder's Handbuch der Entomologie (1921) and have been frequently reproduced in geological and entomological texts, are highly imaginative and misleading. Since Handlirsch did not examine the actual specimens which he restored, the results could hardly have been otherwise. The restoration of *Mischoptera* included here (figure 3) is necessarily incomplete and shows only those structures actually preserved in specimens of the family.

Unfortunately, nothing is known of the immature stages of the Commentry Megasecoptera. Nymphal forms of Brodiidae, with wing pads in various stages of development, have been found together with adults, in Carboniferous strata of England. This record, along with the wing and body structure, seems to refute Forbes' contention (1943) that all Megasecoptera were Holometabola, a conclusion apparently based on the arrangement of veins constituting the radial sector.

Family ASPIDOTHORACIDAE

Systematic descriptions.—This family, which contains only one genus, was established by Handlirsch (1919). Since his diagnosis of it was very brief and included some characteristics not actually present in the fossils, the following diagnosis is proposed for the family:

Wings: The fore and hind wings are alike in venation. Sc terminates well before the apex of the wing. Sc and R1 very close together and submarginal; stem of M very close to R basally but separate from it; MA free from Rs and not diverging towards it; stem of Cu very close to that of M, but not fused with it; CuA not diverging towards MP; one anal vein. Cross-veins numerous and nearly uniformly distributed over the wing area.

Body: Prothorax with a conspicuous, thickened notum, much broader than longer, and armed with stout spines. Fore and middle legs slender; abdomen of moderate size, with long cerci and a pair of terminal claspers in the male.

Genus ASPIDOTHORAX Brongniart

Aspidothorax BRONGNIART, 1894, Recherches Hist. Ins. Foss., p. 304; HANDLIRSCH, 1906, Foss. Ins., p. 315; LAMEERE, 1917, Mus. Nat. Hist. Natur., Bull., vol. 23, p. 146.

Wings: Rs arising before the middle of the wing, with three to five terminal branches; MA arising basad of the origin of Rs, unbranched; MP forked; CuA unbranched; CuP unbranched or forked; 1A with five to seven veinlets along the wing margin.

Genotype: Aspidothorax triangularis Brongniart.

Brongniart erected this genus for two species, *triangularis* and *maculatus*, from the Commentry shales. His definition of the genus is satisfactory in most respects, but requires modification in details, which are especially clear in a specimen (no. C1) collected after Brongniart's account was published. This fossil shows that the subcosta, instead of terminating near the apex of the wing, as Brongniart thought, really ends in the pterostigmal area. Another typically megasecopterous feature of *Aspidothorax*, not mentioned by Brongniart, is the nature of the basal connections of the media and cubitus. The stem of M, although contiguous with the proximal part of R, is actually distinct from it; as M diverges from R, it is connected to it by a short cross-vein, as in the Protohymenidae and related families. The stem of Cu is likewise distinct from that of M.

ASPIDOTHORAX TRIANGULARIS Brongniart
Figure 1

Aspidothorax triangularis BRONGNIART, 1894, Recherches Hist. Ins. Foss., p. 306, pl. 17, figs. 4–6; HANDLIRSCH, 1906, Foss. Ins., p. 315; LAMEERE, 1917, Mus. Nat. Hist. Natur., Bull., vol. 23, p. 146; HANDLIRSCH, 1919, Denkschr. Akad. Wiss., vol. 96, p. 69, fig. 80.

Aspidothorax maculatus BRONGNIART, 1894, Recherches Hist. Ins. Foss., p. 307, pl. 17, fig. 7 [nec 8]; HANDLIRSCH, 1906, Foss. Ins., p. 315; LAMEERE, 1917, Mus. Nat. Hist. Natur., Bull., vol. 23, p. 146 (synonymy with *triangularis*); HANDLIRSCH, 1919, Denkschr. Akad. Wiss., vol. 96, p. 70, fig. 82.

Aspidothorax nanus HANDLIRSCH, 1919, Denkschr. Akad. Wiss., vol. 96, p. 70, fig. 81.

This species was based upon two specimens. One (17-4) consists of a complete insect with wings outspread and showing the general form of the thorax and abdomen. The venation is very clear in all wings, although only crudely shown in Brongniart's figure. It is the only specimen of the species in which both fore and hind wings are satisfactorily preserved. The other specimen, 17-5, shows a nearly complete hind wing, the proximal portions of the other wings and vague outlines of the thorax and abdomen. The specimen of *maculatus* (17-7) consists of a well preserved hind wing, parts of a fore wing and fragments of the thorax. Apart from these types, there is the additional specimen mentioned above, consisting of the two fore wings, the pronotum, and parts of the prothoracic legs.

The following account of *triangularis* is based on these four fossils.

Fore wing: Length, 31 mm.; width, 8 mm.; moderately slender, widest beyond middle. Cross-veins arranged as shown in figure 1.

Hind wing: Length, 20 mm. in 17-4, 32 mm. in 17-5, 35 mm. in 17-7; width, 8–8.5 mm. The wing is shaped very much like the fore wing, but is slightly broader proximally, 1A being more remote from the margin than in the fore wing.

Both fore and hind wings had markings, which can be seen in all specimens. Their distribution on the wings is shown in figure 1. It should be noted that although Brongniart indicated the small maculations in his composite drawing (figure 6, plate 17), he omitted the large apical macule.

Body: Nothing is known of the head, although parts of it may be poorly preserved in specimen 17-4. The body as a whole, exclusive of head and cerci, is 22 mm. long. The pronotum, which is best shown in specimen no. C1, is very unusual. It is about twice as wide as long, with the oblique lateral margins bearing five stout spines, and all margins thickened. The fore legs, which were apparently attached anteriorly, as in the Protodonata, extend 9 mm. beyond the edge of the pronotum. The tarsal segmentation is not indicated. In specimen 17-7 the front legs are crossed in front of the head in such a way as to resemble a large pronotum, and they were so drawn by Brongniart. The middle legs, which are about the same length as the fore pair, are similarly arranged in specimen 17-4, though not shown in Brongniart's drawing. The abdomen, preserved only in the same fossil, is 14 mm. long and 6 mm.

wide, and shows eight segments distinctly. Lameere believed he could distinguish a strong spine on the posterior angle of the sides of each abdominal segment, but I was unable to find any indications of these. The abdomen appears to have been slightly crushed, however, during preservation of the specimen, and the joints between segments

Brongniart has been discussed by both Handlirsch and Lameere. I agree entirely with the latter that *maculatus* is a synonym of *triangularis*, Brongniart having incorrectly interpreted and drawn the radial sector of specimen 17-7, on which he based *maculatus*. Handlirsch, who saw none of the actual fossils, established his two species on

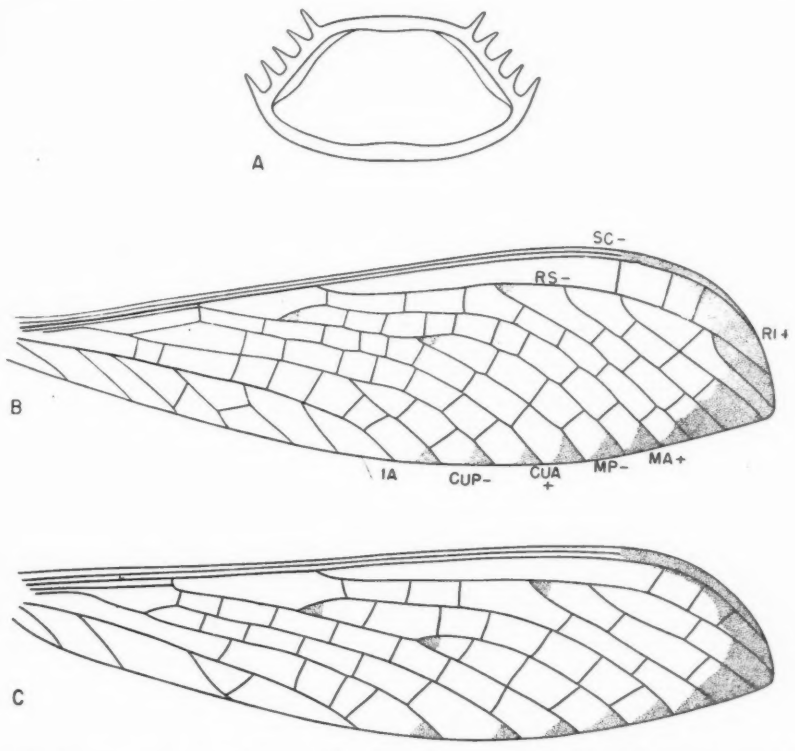


FIG. 1—*Aspidothorax triangularis* Brongniart. A, prothorax (dorsal view) of specimen C1; B, fore wing of same specimen; C, hind wing of specimen 17-4. Sc, subcosta; R1, radius; Rs, radial sector; MA, anterior media; MP, posterior media; CuA, anterior cubitus; CuP, posterior cubitus; 1A, first anal; −, concave veins; +, convex veins.

are unusually prominent, especially laterally. Posterior to the last (8th) distinct tergite there is an obscure plate which seems to bear a pair of curved processes, very similar to the ones present in the Protohymenidae (Megasecoptera) and the Ephemerida (see Carpenter, 1939, fig. 2.). The proximal portion of one cercus, about 7 mm. long, is also preserved. The complete cerci were probably as long as those of *Psilothorax* and *Mischoptera*.

Synonymy.—The status of *maculatus* the basis of Brongniart's illustrations. *Nanus* was based on specimen 17-4, one of the cotypes of *triangularis*, on the grounds that Brongniart's figure showed that it differed in venational details from the other type of *triangularis*. As I have mentioned above, however, Brongniart's drawing of specimen 17-4, which was the best *Aspidothorax* he had, was crudely done. The fossil itself does not support Handlirsch's action, —which, incidentally, is really ludicrous since he cites as exemplifying the true

triangularis a drawing (17-6) based mainly on specimen 17-4. Handlirsch's other species, *dubius*, was based on specimen 17-8, with the statement that it probably does not belong to *Aspidothorax*. I agree with this and furthermore feel that the very poor condition of the fossil justifies its assignment to Insecta Incertae Sedis.

Affinities.—The family Aspidothoracidae appears to be most closely related to the Bardohymenidae, from the Lower Permian of Oklahoma and later Permian of Russia. Both families have the crowding of Sc, R1 and the stems of M and Cu; as well as the independence of Rs and MA, and MP and CuA. Cross-veins are fewer in the Bardohymenidae, but those present are nearly uniformly distributed over the wing. More remotely related are the Permian Protohymenidae and Scytohymenidae, which are specialized by further crowding of the veins mentioned and by anastomosis of MA and MP with Rs and CuA respectively.

Family MISCHOPTERIDAE

Systematic descriptions.—This family was established by Handlirsch (1906) for four genera and many species, all from Commentry. Study of Brongniart's original type material and additional specimens, subsequently collected, convinces me that the diagnosis of the family needs revision and that only two genera should be included, the others being assigned elsewhere. The following diagnosis is proposed:

Wings: Venation of fore and hind wings similar. Sc remote from margin and terminating before the apex of the wing; R and R1 remote from Sc, the subcostal and costal spaces being of equal widths; stem of M very close to R basally but separate from it; MA anastomosed for a short distance with Rs, near the latter's origin; stem of Cu removed from that of M; CuA independent of MP and not diverging towards it; one anal vein. Cross-veins regularly arranged, close together in costal and subcostal areas, but forming two or three rows over most of wing.

Body: Prothorax short, with or without lateral spines; fore legs very short; abdomen slender, about as long as wings; cerci elongate, fully twice as long as abdomen.

Genus MISCHOPTERA Brongniart

Woodwardia BRONGNIART, 1885 (nec Crosse and Fischer, 1861), Soc. Amis Sci. Nat. Rouen, Bull., vol. 21, p. 64.

Mischoptera BRONGNIART, 1894, Recherches Hist. Ins. Foss., p. 283; HANDLIRSCH, 1906, Foss. Ins., p. 316.

Wings: Both fore and hind wings falcate, the hind pair more strongly so. Rs arising well before the middle of the wing, with three terminal branches, all other veins unbranched; cross-veins in costal and subcostal areas about as far apart as their lengths; cross-veins between other main veins strongly sigmoidal, and arranged so as to form three rows over at least part of the wing. Large nygmata-like spots occur regularly at certain places on both fore and hind wings.

Genotype: *Mischoptera nigra* Brongniart

MISCHOPTERA NIGRA Brongniart

Figures 2 and 3, and plate 53, figure 1

Mischoptera nigra BRONGNIART, 1885, Soc. Amis Sci. Nat. Rouen, Bull., vol. 21, p. 64, pl. 2, fig. 2, pl. [4], fig. 1.

Mischoptera nigra BRONGNIART, 1894, Recherches Hist. Ins. Foss., p. 287, pl. 13, fig. 3; HANDLIRSCH, 1906, Foss. Ins., p. 317, pl. 33, fig. 2; LAMEERE, 1917, Mus. Nat. Hist. Natur., Bull., vol. 23, p. 142; HANDLIRSCH, 1919, Denkschr. Akad. Wiss., vol. 96, p. 71.

Mischoptera woodwardi BRONGNIART, 1894, Recherches Hist. Ins. Foss., p. 286, pl. 13, figs. 1, 2, 4, 5, 6, 7; HANDLIRSCH, 1906, Foss. Ins., p. 317, pl. 33, fig. 1; LAMEERE, 1917, Mus. Nat. Hist. Natur., Bull., vol. 23, p. 142; HANDLIRSCH, 1919, Denkschr. Akad. Wiss., vol. 96, p. 71.

Mischoptera concolor HANDLIRSCH, 1919, Denkschr. Akad. Wiss., vol. 96, p. 71.

Mischoptera ocellata HANDLIRSCH, 1919, Denkschr. Akad. Wiss., vol. 96, p. 71.

Mischoptera infumata HANDLIRSCH, 1919, Denkschr. Akad. Wiss., vol. 96, p. 71.

Although originally based on two fossils, this species is now known from ten specimens, two of which were found after the publication of Brongniart's *Recherches*. These are sufficient to give us a reliable and general conception of this remarkable insect (figure 3).

Wings: The fore wing, which is completely preserved in several specimens, is from 73 to 75 mm. long, with a maximum width of 20 mm. The details of the venation are shown in figure 2, which is based upon one of the specimens (C2) not seen by Brongniart. The form of the main veins is sur-

prisingly constant; Rs has three terminal branches, and the other veins are unbranched in all specimens. The sigmoidal cross-veins are much more variable in position, though three distinct series of them are always maintained. The nygmata-like spots are arranged in two rows of three each, with a seventh placed distally and medially with respect to the rows, as indicated in the figure. These structures are obviously not pigment spots; they appear as slight swellings, having a texture different from that of the rest of the wing membrane. There is certainly no reason to believe that they are homologous with the nygmata of holometabolous insects. The hind wing is about 5 mm. longer than the fore wing, and slightly broader. It is also more markedly falcate than the fore wing, but shows no venational differences.

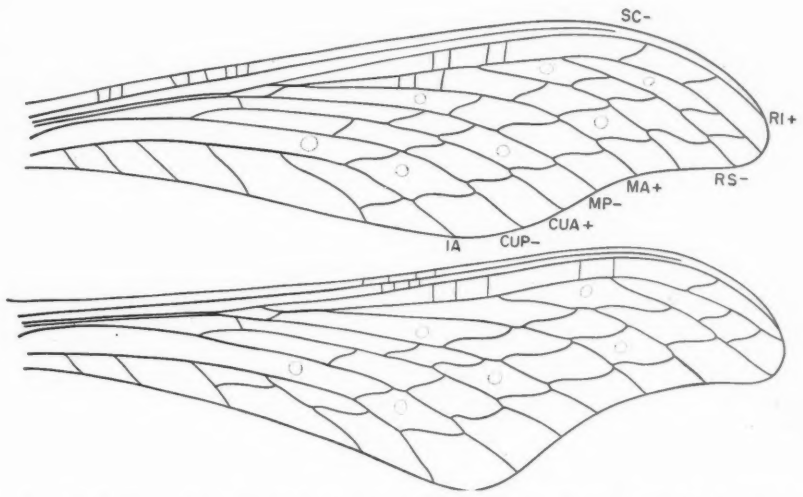


FIG. 2—*Mischoptera nigra* Brongniart. Fore and hind wings of specimen C2. Lettering as in figure *1*.

Body: The head and prothorax of *nigra* have been incorrectly interpreted by both Handlirsch and Brongniart. Brongniart's specimen 13-1 and also one of the new fossils (C2), show that the head was relatively small, about 4.5 mm. long and broad, as seen from above. The position of the antennae in the two specimens mentioned indicates that the head was hypognathous, the mouth-parts being hidden from view. The antennae are 18 mm. long and tapering; their segmentation is not discernible. The prothoracic legs, which Brongniart and Handlirsch confused with part of the head, are very short, extending only 9.3 mm. beyond the thorax. The femur is short and broad, visible for only about 4 mm. beyond the thorax. The junction of the tibia and tarsus is not discernible in any specimen, but the combined lengths of these segments is only 5 mm. In the several specimens in which they are preserved, the fore legs are curved around the head and resemble the raptorial legs of certain aquatic Hemiptera, as pointed out by Lameere. Whether they were actually raptorial or not remains questionable; there is certainly nothing else about *Mischoptera* suggestive of predaceous habits. In none of the specimens of *nigra* are there even fragments of the meso- and metathoracic legs. Their complete absence, especially in such a well preserved specimen as that shown in plate 53, figure 1, is difficult to explain. Possibly they were short, like the fore legs, and were therefore concealed by the body proper.

The meso- and metathoracic segments were nearly alike; as preserved, they are 9 mm. long and 10 mm. wide. The abdomen is relatively slender, being 67 mm. long and 8 mm. wide. Each abdominal segment shows a median longitudinal ridge and the last

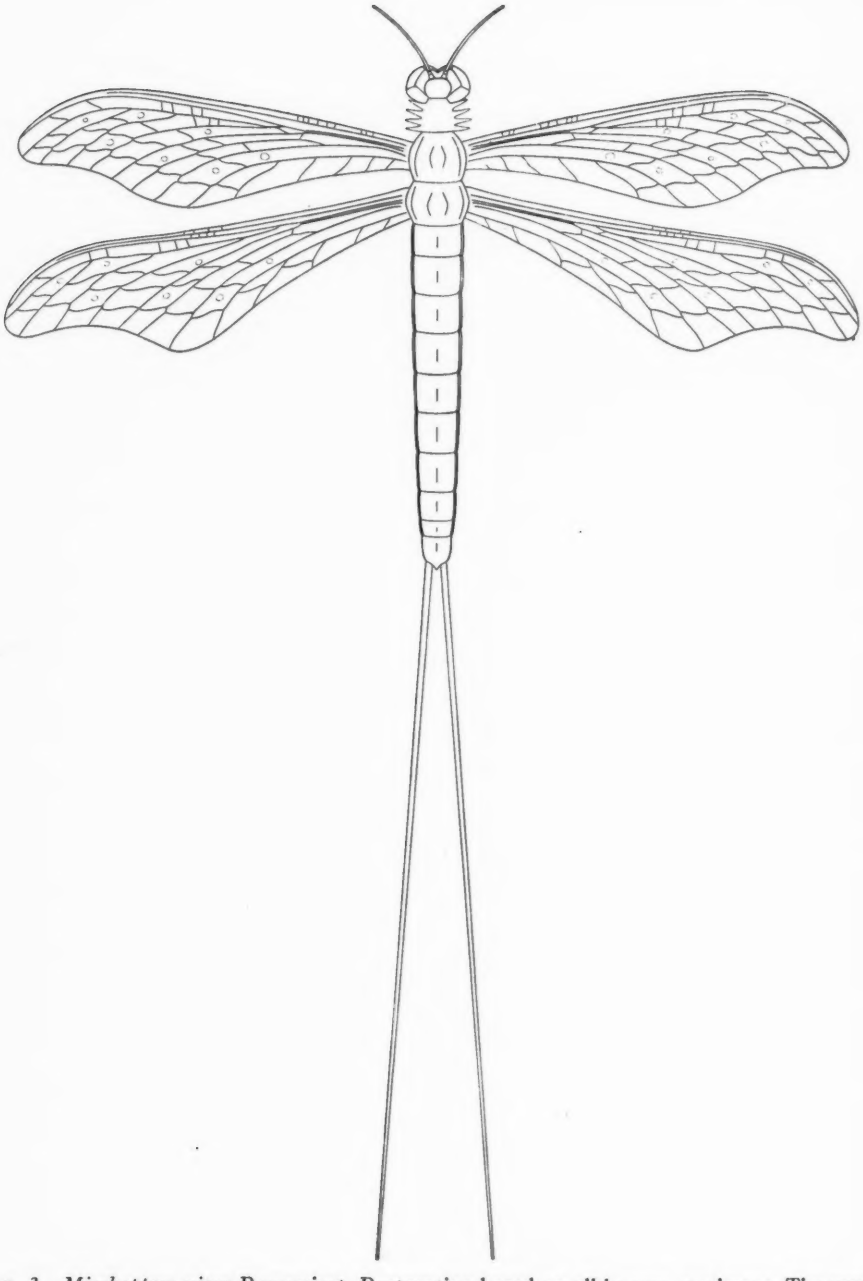


FIG. 3—*Mischoptera nigra* Brongniart. Restoration based on all known specimens. The meso- and metathoracic legs are unknown.

tergite has a small, median terminal projection. Only the proximal parts of the cerci are preserved (specimen 13-3), but the dimensions of the preserved portions indicate that the cerci were about as long as those of the closely related *Psilothorax*, in which they were considerably longer than the entire body. In the restoration of *nigra* shown in figure 3, the cerci have been extended to a similar length.

Synonymy.—Of the two specimens on which Brongniart originally (1885) based this species, the one depicted in his figure 2, plate 2, was later (1894) placed by him in the second species, *woodwardi*. He distinguished these two species by the differences in the arrangements of cross-veins: in *woodwardi* these were supposedly arranged in three rows, instead of two, as in *nigra*. As Lameere has pointed out, however, this difference does not actually exist, the unique specimen of *nigra* (13-1) having the three rows of cross-veins, also. The blackness of the specimen of *nigra* is clearly a matter of preservation, since the Commentry insects in general vary greatly in this respect, regardless of species.

Handlirsch's new species (*concolor*, *ocellata* and *infumata*) were erected for three of the type specimens of *woodwardi*. These were based solely on Brongniart's figures and on such characteristics as the color of the wings, presence or absence and the position of the "nygmata," and the arrangement of cross-veins. None of the distinctions indicated by Handlirsch are valid. The nygmata-like structures, which appear as slight swellings in the membrane, are present in all specimens (though only faintly preserved in a few), and they occupy the same position in all wings. Similarly, the cross-veins show only a normal range of variation, like that in the Neuroptera, Odonata and other insects with a full venation. If Handlirsch had examined the actual specimens, he probably would not have named any of these three species.

Mischoptera nigra is one of the most remarkable of the Commentry Megasecoptera. The short and modified fore legs, armed prothorax and falcate wings are highly specialized features, unexpected in a Carboniferous insect.

Genus PSILOTHORAX Brongniart

Psilothorax BRONGNIART, 1894, Recherches Hist. Ins. Foss., p. 288; HANDLIRSCH, 1906, Foss. Ins., p. 317.

Wings: Fore wing with an evenly rounded posterior margin; hind wing slightly falcate, and broader than fore wing. Rs arising about one-quarter of the wing-length from the base, with three terminal branches; all other veins unbranched; amount of anastomosis of Rs and MA greater than in *Mischoptera*, the free basal piece of MA being very short; costal and subcostal cross-veins apparently as in *Mischoptera*, but very weak; cross-veins between other main veins long and slightly sigmoidal, arranged to form two rows. "Nygmata" appear to be absent.

Genotype: *Psilothorax longicauda* Brongniart.

PSILOTHORAX LONGICAUDA (Brongniart)
Figure 4

Woodwardia longicauda BRONGNIART, 1885, Soc. Amis Sci. Nat., Bull., vol. 21, p. 64.

Psilothorax longicauda BRONGNIART, 1894, Recherches Hist. Ins. Foss., p. 289; pl. 13, figs. 8–12; pl. 15, figs. 1–4; HANDLIRSCH, 1906, Foss. Ins., p. 318, pl. 32, fig. 16; LAMEERE, 1917, Mus. Nat. Hist. Natur., Bull., vol. 23, p. 143.

Psilothorax pictus HANDLIRSCH, 1919, Denkschr. Akad. Wiss., vol. 96, p. 72.

This species was based on three specimens one of which (13-8) shows all four wings and much of the body.

Wings: These are relatively shorter and broader than the wings of *Mischoptera nigra*. The fore wing, which is complete in specimen 13-8, is 62 mm. long and 18 mm. wide (maximum). The hind wing, preserved in specimen 13-8, is completely known except for its very apex. It is about the same length as the fore wing and has a maximum width of 20 mm. The venation of both wings is represented in figure 4. This was correctly depicted by Brongniart, except that the subcosta does not extend so far distally as shown in his drawings, and the radius terminates just before the apex of the wing. In both of these respects, the venation is more like that of *Mischoptera* than might be inferred from Brongniart's figures. The anastomosis of MA and Rs is also much as in *Mischoptera*, though the basal piece of MA, before the anastomosis,

is shorter and the amount of anastomosis is greater. The sigmoidal cross-veins are arranged in two rows, instead of three as in *Mischoptera*. In the fore wing there is a sigmoidal cross-vein between R1 and Rs before the first fork of the latter; this is not apparent in the hind wing. There are only faint indications of cross-veins in the costal and subcostal areas. Neither wing shows in one of the fossils. The prothorax shows no indications of lateral spines; had they been present, I believe they would be visible in specimen 13-8, which is well preserved. The pterothorax and the abdomen, which is 62 mm. long, closely resemble those of *Mischoptera*. Both cerci are preserved in two specimens. In one, they are fully 72 mm. long before reaching the edge

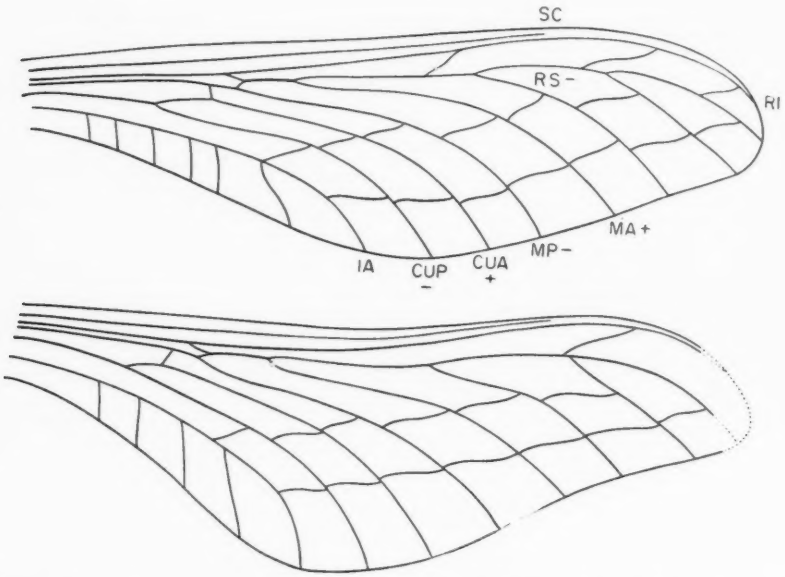


FIG. 4—*Psilothorax longicauda* Brongniart. Fore and hind wings, drawing based mainly on specimen 13-8. Lettering as in figure *1*.

any indication of the nygmata-like spots so distinctly preserved in most specimens of *Mischoptera*.

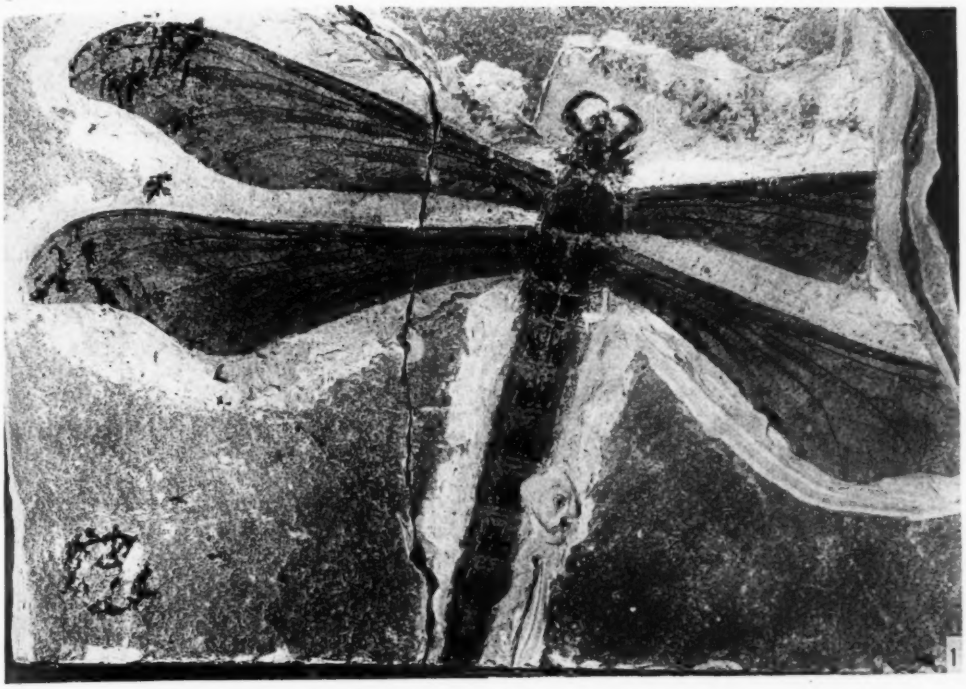
Body: The thorax and part of the head are preserved in specimens 13-8, 13-9, and 13-10. As noted by Lameere, Brongniart misinterpreted the head structure; the fore legs, which are formed precisely like those of *Mischoptera*, are curved laterally around the head. However, I have not been able to discern the mandibles that Lameere described of the rock fragment which contains the fossil. Brongniart's specimen 13-10, which consists only of the end of the abdomen and the cerci, may belong to *longicauda*, but since this cannot be proven, I suggest that it be referred to Incertae Sedis under the Order Megasecoptera.

Synonymy.—Handlirsch (1919) established *Ps. pictus* for Brongniart's specimen 13-12, without giving any reason for doing so. Since I have not been able to discover

EXPLANATION OF PLATE 53

FIG. *1*—Photograph of *Mischoptera nigra* Brongniart, specimen C2, Museum National d'Histoire Naturelle, Paris, ×0.85. (p. 340)

2—Photograph of *Sphecoptera brongniarti* Meunier, type specimen, Museum National d'Histoire Naturelle, Paris, ×1.75. (p. 346)



Carpenter, Carboniferous insects from Commentry

notable differences between this fossil and the other Brongniart specimens, I have placed *pictus* in synonymy.

Affinities.—The family Mischopteridae, which includes the largest and most spectacular of the Megasecoptera, is more specialized than the Aspidothoracidae in nearly all respects, although there is less crowding of the anterior veins. The serial arrangement of the cross-veins and the anastomosis of Rs and MA are suggestive of the Protohymenidae and other Permian families, as well as the Sphecopteridae. The falcate wings and nygmata-like structures of *Mischoptera* are apparently not family traits, but specializations attained by a particular group of its species.

Sphecoptera and *Cyclocelis*, which have formerly been placed in the Mischopteridae. However, the wing shape, termination of Sc on R1 and the arrangement of cross-veins seem to me to require a separate family.

Genus SPHECOPTERA Brongniart

Sphecoptera BRONGNIART, 1894, Recherches Hist. Ins. Foss., p. 294; HANDLIRSCH, 1906, Foss. Ins., p. 318; LAMEERE, 1917, Mus. Nat. Hist. Natur., Bull., vol. 23, p. 144; HANDLIRSCH, 1919, Denkschr. Akad. Wiss., vol. 96, p. 72.

Wings: Very slender, Rs arising well before mid-wing, with three terminal branches; all other veins unbranched; cross-veins slightly sigmoidal, one between each

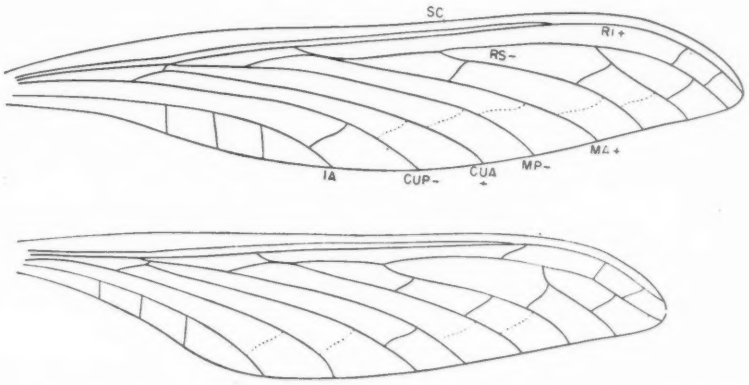


FIG. 5—*Sphecoptera gracilis* Brongniart. Fore and hind wings of specimen 16–5. Veins not preserved are represented by broken lines. Lettering as in figure *1*.

SPHECOPTERIDAE, new family

Systematic descriptions.—Allied to the Mischopteridae. Wings slender, petiolate, and the venation of fore and hind wings similar. Sc remote from margin and terminating on R1 a short distance beyond mid-wing; R closer to Sc than in Mischopteridae; stem of M coalesced with R; MA usually anastomosed with Rs for a very short distance, rarely (hind wing only) diverging toward Rs and not quite touching it; stem of Cu remote from R+M; CuA independent of MP; one anal vein. Cross-veins apparently absent from costal and subcostal areas, but forming only one complete row in the main part of the wing.

This family is established for the genera of the main veins, the series forming a regular row; additional cross-veins, farther proximally between Rs and MA, MA and MP, and occasionally between the branches of Rs. Both wings with conspicuous maculations.

Genotype: *Sphecoptera gracilis* Brongniart

SPHECOPTERA GRACILIS Brongniart
Figure 5

Sphecoptera gracilis BRONGNIART, 1894, Recherches Hist. Ins. Foss., p. 294, pl. 15, figs. 5–6; HANDLIRSCH, 1906, Foss. Ins., p. 319, pl. 33, fig. 9; HANDLIRSCH, 1919, Denkschr. Akad. Wiss., vol. 96, p. 72.

This species was based on three fossils, shown in figures 5, 6, and 7 of Brongniart's plate 16. The fossil represented in figure 6

is almost certainly a counterpart of that shown in figure 5, but since it could not be found in the Museum collection in 1938, my conclusion is based on Brongniart's drawing. If I am correct, the species is known only from one specimen, for the very poorly preserved fossil shown in Brongniart's figure 7 includes so little of the venation that assignment even to the family Sphecopteridae is questionable.

The following account of *gracilis* is based on specimens 15-5 and 15-6:

Wings: The fore wing is 57 mm. long and 10 mm. wide (maximum); the hind wing has the same width but it is slightly shorter with a length of 50 mm. The venation of the fore and hind wings is shown in figure 5. In both pairs R2+3 is forked and R4+5 unbranched, but these may be individual instead of specific traits. CuA is joined by a cross-vein to M or R+M just before the separation of R and M. The cross-veins are not satisfactorily preserved, but they were probably arranged as in *brongniarti* Meun., with one sigmoidal cross-vein between most longitudinal veins. In the hind wing, however, there is a cross-vein between R1 and Rs which is not known in other species of the genus. The wing maculations are only faintly indicated but appear to be like those of *brongniarti*.

Brongniart's illustration of *gracilis* (plate 15, figure 5) seems entirely correct except that it exaggerates slightly the petiolation of the wing. Handlirsch's figure (1906), a crude copy of Brongniart's, further exaggerates the petiolation of the fore wing and includes cerci found in another fossil (15-7).

The specimen of *gracilis* seems to have deteriorated greatly since Brongniart studied it, for I was able to discern only faint indications of abdominal segments. In view of what is known of other sphecopterids, it seems certain that his figure does not correctly represent the head.

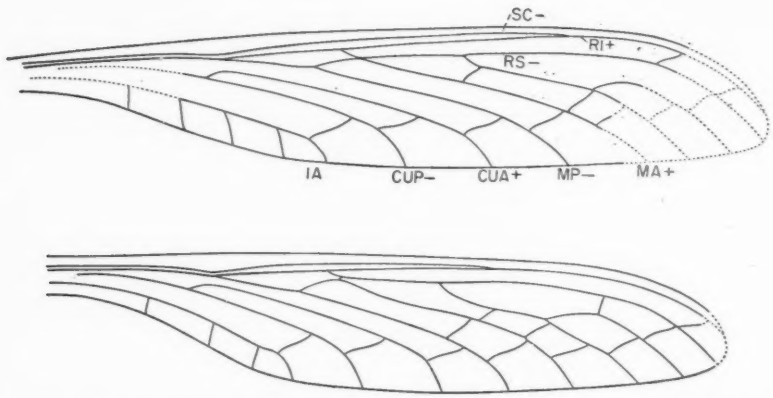


FIG. 6—*Sphecoptera brongniarti* Meunier. Fore and hind wings of type. Lettering as in figure 1.

SPHECOPTERA BRONGNIARTI Meunier
Figure 6 and plate 53, figure 2

Sphecoptera brongniarti MEUNIER, 1908, Mus. Nat. Hist. Natur., Bull., vol. 14, p. 248, fig. 4; MEUNIER, 1909, Ann. Paleont., vol. 4, p. 142, fig. 13, pl. 2, fig. 6; LAMEERE, 1917, Mus. Nat. Hist. Natur., Bull., vol. 23, p. 144.

This species was based on a single, well preserved specimen, consisting of three nearly complete wings, part of the fourth, and some of the body. It is by far the best specimen of a sphecopterid known.

Wings: The fore wing, which lacks the apical portion, is 38 mm. long; the complete length was probably about 42 mm. The hind wing is 37 mm. long, virtually complete. Both fore and hind wings have a maximum width of 7 mm. The fore wing is clearly somewhat longer than the hind and

its petiolation is not so extreme. The venation is very similar in both pairs of wings, even to the forking of R4+5. MA has slight contact with Rs in the fore wing, as in *gracilis*, but in the hind wing these veins do not actually meet, though connected by a short cross-vein. CuA is not joined by a cross-vein to the stem of M as in *gracilis*. Slight variation apparently exists in the arrangement of cross-veins: in the fore wing, there is only a single cross-vein between all main veins, except in the area between MA and Rs, whereas in the hind wing there are also two cross-veins between MA and MP and R2+3 and R1. The maculations, which are clearly shown in the photograph (plate 53, figure 2), are arranged in transverse rows.

Body: The head is not preserved, and there is only a small fragment of the prothorax, but some other parts of the body are clear. The pterothorax is 5.5 mm. long. The abdomen, which is 25 mm. long and 2.5 mm. wide, shows ten segments and bears a pair of cerci 4.5 mm. long, between which the last abdominal segment is prolonged, as in *Mischoptera*.

Meunier's figure of this fossil (1908, 1909) is misleading; the shape of the fore wing is incorrectly represented and most of the cross-veins are omitted. Also, the hind wing is 37 mm. long, not 50 mm., as Meunier states.

SPHECOPTERA MINOR (Brongniart)

Cyclocelis minor BRONGNIART, 1894, Recherches Hist. Ins. Foss., p. 291, pl. 15, fig. 9; HANDLIRSCH, 1906, Foss. Ins., p. 318, pl. 33, fig. 6.
Sphecoptera minor LAMEERE, 1917, Mus. Nat. Hist. Natur., Bull., vol. 23, p. 144.

This species was based on a single specimen (15-9), consisting of two fore wings and one hind wing. None of these wings is complete and the preservation of the fossil as a whole is poor.

Wings: The fore wing is 40 mm. long and 9 mm. wide; the hind wing 35 mm. long, as it is preserved. This specimen must have deteriorated since Brongniart's time, for I have not been able to make out nearly as much of the venation as he shows in his drawing. However, the venation is obviously like that of *gracilis*, including the unforked MP. The fore wing is relatively broader than that of *gracilis* and the maculations are larger. These two features, added to the smaller size of the wings, appear to justify the retention of the species as distinct from *gracilis*.

Brongniart omitted from his drawing of the left fore wing one branch of Rs, though this is shown in the opposite fore wing. Since Handlirsch's figure (1906) was based on Brongniart's, it is also incorrect in this respect.

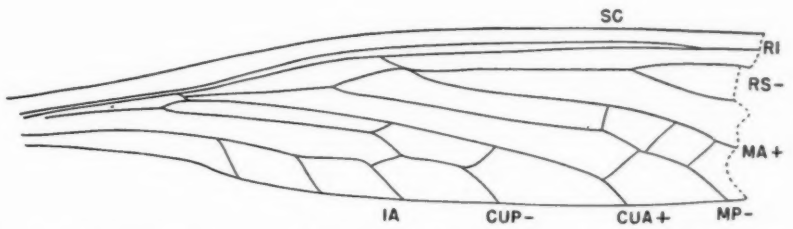


FIG. 7—*Sphecoptera elegantissima* (Meunier). Type specimen. Lettering as in figure *1*.

SPHECOPTERA ELEGANTISSIMA (Meunier)
Figure 7

Cyclocelis elegantissima MEUNIER, 1908, Mus. Nat. Hist. Natur., Bull., vol. 14, p. 249, fig. 5; MEUNIER, 1909, Ann. Paleont., vol. 4, p. 142, pl. 2, fig. 5.
Sphecoptera elegantissima LAMEERE, 1917, Mus. Nat. Hist. Natur., Bull., vol. 23, p. 144.

This species was established on a well preserved, incomplete fossil, consisting of the proximal three-fourths of one wing and about one-third of another. The largest fragment is 32 mm. long and 7 mm. wide, indicating a full length of 42 mm. The wing has a slightly arched anterior border and a petiolation like that of *brongniarti*. The venation (as well as maculations) is also

like that of *brongniarti*, except that CuA is very close to M proximally and is connected to it by a cross-vein. There are two cross-veins between CuP and MA, but this number may well be subject to individual variation. This species may be the same as *brongniarti*, but since we know nothing of the venational variation of the sphecopterids, it seems advisable to let the species stand.

Meunier's drawing of *elegantissima* is very inaccurate. He depicts much more anastomosis of Rs and MA than actually exists in the fossil, and has drawn the end of CuP as the anal vein, in addition to omitting most cross-veins.

Genus CYCLOCELIS Brongniart

Cyclocelis BRONGNIART, 1894, Recherches Hist. Ins. Foss., p. 290; HANDLIRSCH, 1906, Foss. Ins., p. 319.

Wings: Moderately slender, much broader than those of *Sphecoptera*. Rs arising nearer mid-wing than in *Sphecoptera*, with three terminal branches; MP deeply forked, all other veins unbranched; cross-veins straight, arranged essentially as in *Sphecoptera*. Both wings have maculations.

Genotype: Cyclocelis chatini Brongniart

This genus differs from *Sphecoptera* in several respects, notably in having a forked MP. Handlirsch, who synonymized it with *Sphecoptera*, was unaware of the validity of this feature, though it was mentioned by Brongniart.

CYCLOCELIS CHATINI Brongniart
Figure 8

Cyclocelis chatini BRONGNIART, 1894, Recherches Hist. Ins. Foss., p. 291, pl. 16,[1] figs. 1, 2, 3; HANDLIRSCH, 1906, Foss. Ins., p. 318, pl. 33, figs. 3, 4, 5; LAMEERE, 1917, Mus. Nat. His. Natur., Bull., vol. 23, p. 143.

Sphecoptera chatini HANDLIRSCH, 1919, Denkschr. Akad. Wiss., vol. 96, p. 72.

Sphecoptera brongniartiana HANDLIRSCH, 1919, Denkschr. Akad. Wiss., vol. 96, p. 72.

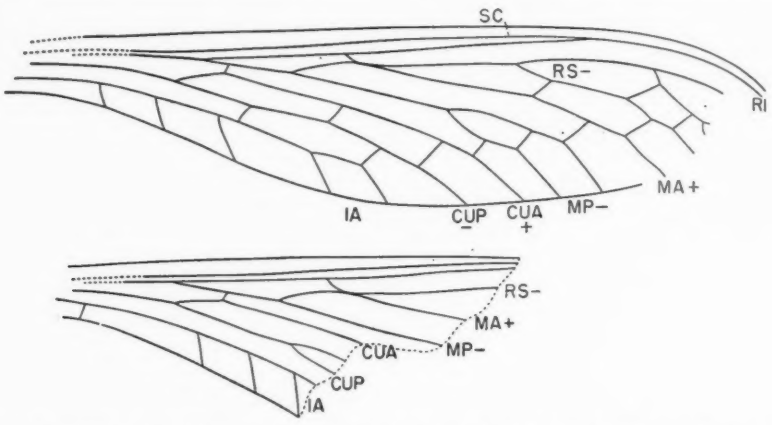


FIG. 8—*Cyclocelis chatini* Brongniart. Fore and hind wings of specimen 16-1. Lettering as in figure *1*.

Sphecoptera fenestrata HANDLIRSCH, 1919, Denk. schr. Akad. Wiss., vol. 96, p. 72.

This species was based on three fossils, depicted on Brongniart's plate 16, figures 1–3. One of these (16-1) consists of a fore wing and basal portions of the other three wings, with vague indications of the prothorax and mesothorax. One of the others (16-2) consisted of a single wing, lacking the base; the third (16-3) included portions of three wings. The two latter specimens I could not find in the Museum in 1938, nor could I locate the additional fossil which Lameere mentioned in 1917. Fortunately, the remaining type (16-1) is sufficiently well preserved to enable us to determine the structure of the fore wing and part of the hind.

Wings: Fore wing, 55 mm. long and 13 mm. wide; hind wing apparently a little shorter than the fore. Venation of fore wing as in figure 8. The outer series of cross-

[1] These three figures were mislabeled *maculata* in the explanation of plate 16.

veins is complete, but the inner series is incomplete, with no cross-veins between MA and MP, MP and CuA. The venation of the hind wing is like that of the fore; in specimen 16-1 there is an indication of a twig on CuP which is not present in the hind wing of 16-3.

Body: This is almost completely unknown. I have been unable to discern in the fossil the portions of the prothorax shown in Brongniart's figure of 16-1. Lameere stated that in a new specimen of this insect, which I was unable to find in the collection, the prothorax was long, like that of *Aspidothorax*, but lacked spines. Nothing is known of the rest of the body.

Synonymy.—Handlirsch established his two species on Brongniart's figures of the two fossils (16-2 and 16-3), without mentioning or indicating the character of the species. Since I can see no basis for their separation, I place both in synonymy with *chatini*.

CYCLOCELIS OBSCURA Brongniart

Cyclocelis obscura BRONGNIART, 1894, Recherches Hist. Ins. Foss., p. 293, pl. 16, figs. 4, 5.

This species was established for two fossils, shown on Brongniart's plate 16, figures 4 and 5. The latter is so poorly preserved that the wing veins are not even faintly indicated; hence there is no justification for assigning it to *Cyclocelis*. The other specimen, which is represented in Brongniart's figure, consists of a well preserved fore wing and part of the hind, but has so deteriorated that I can make little of it; Brongniart's specific name implies unsatisfactory preservation originally. Since his drawing shows MP forked in both wings, the fossil presumably belongs to *Cyclocelis*. It is larger than *chatini*, however, the fore wing being 64 mm. long as preserved, with a probable length of 70 mm. Brongniart's figure of the hind wing shows MA anastomosed with Rs for some distance, but this was probably the result of erroneous interpretation of the poorly preserved venation.

SPHECOPTERIDAE INCERTAE SEDIS[2]
Sphecopteridarum gen. indet. *acuta* Brongniart

[2] *Sphecoptera distincta* Meunier (1908, Ann. Soc. Sci., Vol. 32, p. 242) is a nomen nudum, no characteristics being mentioned.

Cyclocelis acuta BRONGNIART, 1894, Recherches Hist. Inst. Foss., p. 293, pl. 15, fig. 8; HANDLIRSCH, 1906, Foss. Ins., p. 318, pl. 33, fig. 8.

The fossil on which this species was based consists of four outspread wings, all of which are so badly wrinkled and distorted that the course of the veins cannot be traced. For this reason, it is impossible to determine its generic position and its relation to other species of the family.

Affinities.—The sphecopterids appear to have been derived from a megasecopterous stock more generalized than any actually known. The relatively wide costal space eliminates the Aspidothoracidae as an ancestral line, and suggests the Corydaloididae. However, the latter have an anastomosis of MP and CuA, not even indicated in the sphecopterids. The petiolation of the wings of *Sphecoptera* and *Cyclocelis*, and the termination of Sc on R1 are specializations of this family.

ISCHNOPTILIDAE, new family

Systematic descriptions.—Allied to the Sphecopteridae. Wings slender, petiolate, and venation of fore and hind wings similar, but hind wing narrower than fore. Sc remote from margin (termination unknown); R as close to Sc as in Sphecopteridae; stem of M coalesced with R; MA anastomosed with Rs for a much greater interval than in Sphecopteridae; stem of Cu remote from M; CuA abruptly diverging towards MP and anastomosed with it for a short interval; one anal vein. Cross-veins sigmoidal, forming one complete row.

This family is established for the genus *Ischnoptilus*, formerly placed in the Mischopteridae. The longer anastomosis of Rs and MA, and especially the coalescence of CuA and MP, however, indicate that this genus has evolved much further than even the sphecopterids in the direction of such Permian Megasecoptera as the Protohymenidae.

Genus ISCHNOPTILUS Brongniart

Ischnoptilus BRONGNIART, 1894, Recherches Hist. Ins. Foss., p. 296; HANDLIRSCH, 1906, Foss. Ins., p. 319.

Wings: Rs arising well before mid-wing, with at least three terminal branches; all other veins unbranched; one cross-vein between each main vein, with an extra one

proximally between MP and CuA, and a short one between R1 and Rs at the point of separation of MA from Rs.

Genotype: Ischnoptilus elegans Brongniart

ISCHNOPTILUS ELEGANS Brongniart
Figure 9

Ischnoptilus elegans BRONGNIART, 1894, Recherches Hist. Ins. Foss., p. 297, pl 17, fig. 3; HANDLIRSCH, 1906, Foss. Ins., p. 319, pl. 32, fig. 17; LAMEERE, 1917, Mus. Nat. Hist. Natur., Bull., vol. 23, p. 145.

This interesting species is known only from a type specimen (17-3), consisting of the proximal parts of all four wings and vague outlines of the thorax. As preserved, the right fore wing is 20 mm. long, and 7 mm. wide, but its full length was probably around 26 mm. The hind wing was apparently similar to the fore wing in shape and venation, though not quite so broad. Both pairs of wings were petiolate, resembling those of *Sphecoptera brongniarti* in this respect.

The veins in the preserved parts of the wings are very clear and show strong convexities or concavities, though Brongniart's figure is not accurate. The costal margin of the fore wing is not preserved, but the subcosta and radius are close together, as in the hind wing. The origin of the radial sector is not correctly shown in Brongniart's drawing; it arises at a greater angle than he had indicated and it is joined to the radius shortly after by a prominent, short crossvein. The radial sector has two branches included in the preserved area of the wing. The anterior media is anastomosed with Rs for a considerable distance; in this respect, also, Brongniart's drawing is misleading. The basal connections of the media and cubitus are only faintly indicated in the fore wing, which is broken away at that place, but they are obviously like those of the hind wing, where the structure is very well preserved.

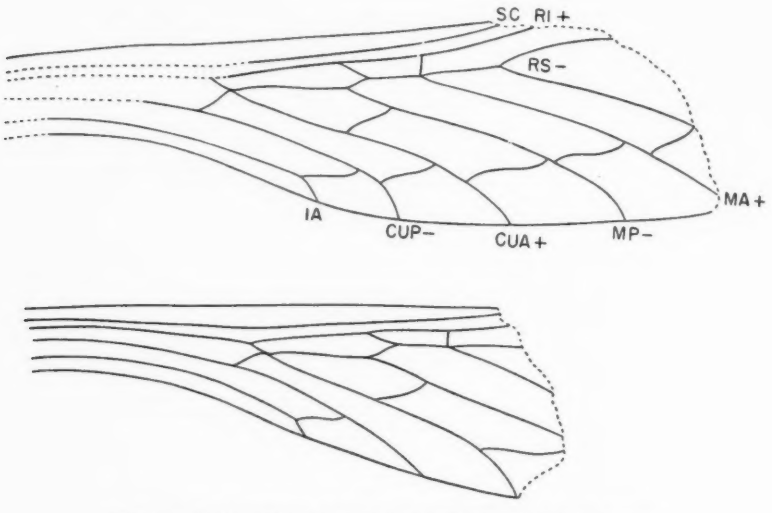


FIG. 9—*Ischnoptilus elegans* Brongniart. Wings of type.

Affinities.—The relationships of the Ischnoptilidae are very uncertain because the wings are incompletely known. They appear to be closest to the Sphecopteridae, but with the added specialization of the anastomosis of CuA with the stem of M,—a peculiarity found also in the Corydaloididae and certain Permian families, such as Protohymenidae and Scytohymenidae.

Family CORYDALOIDIDAE

Systematic descriptions.—This group was established by Handlirsch for the Commentry genus *Corydaloides*. Although the species included undoubtedly require family separation from other known Megasecoptera, they are not as remarkable as Hand-

lirsch indicated. Many of the characteristics which he attributed to them do not actually exist in the fossils. The following is proposed as the diagnosis of the family:

Wings: Fore and hind wings alike in venation, but the hind wing slightly broader basally. Sc remote from the margin and terminating in the costal area well before the apex as in the Mischopteridae; R1 remote from Sc; stem of M coalesced with R; MA anastomosed for a very short interval with Rs, and CuA anastomosed with MP for a longer distance; one anal vein. A few weak cross-veins in costal and subcostal areas; cross-veins between other main veins arranged in three rows.

Body: Abdomen of moderate size, with prominent cerci and with a pair of spines on the posterior lateral corner of each tergite.

Genus CORYDALOIDES Brongniart

Corydaloides BRONGNIART, 1885. Séances Soc. Ent. Fr., Bull., p. 12; BRONGNIART, 1894, Recherches Hist. Ins. Foss., p. 297; HANDLIRSCH, 1906, Foss. Ins., p. 314; LAMEERE, 1917, Mus. Nat. His. Natur., Bull., vol. 23, p. 145.
Corydaliodes HANDLIRSCH, 1919, Denkschr. Akad. Wiss., vol. 96, p. 69.

Wings: Rs arising before mid-wing, with from three to four terminal branches; MP deeply forked, all other veins unbranched, excepting CuP which may be forked. Cross-veins straight or nearly so, with the exception of those above Rs, which are strongly sigmoidal. 1A very remote from wing margin.

Genotype: Corydaloides scudderi Brongniart.

Handlirsch's genus *Corydaliodes* was formed for two of the type specimens of *scudderi*, on the basis of his belief that their bodies seemed to be smaller than those of the others. Since only one of the two showed any part of the body, and that only the thorax, his conclusion appears hardly justified.

CORYDALOIDES SCUDDERI Brongniart
Figure 10

Corydaloides scudderi BRONGNIART, 1885. Séances Soc. Ent. Fr., Bull., pp. 12–13; BRONGNIART, 1885, La Nature, vol. 13, p. 150, figs. 1, 2; BRONGNIART, 1885, Soc. Amis Sci. Nat. Rouen, Bull., vol. 21, p. 64 [plate 4, fig. 3 of reprint]; BRONGNIART 1894, Recherches Hist. Ins. Foss., p. 303, pl. 16, figs. 6, 7, 9–13; HANDLIRSCH, 1906, Foss. Ins., p. 314, pl. 32, fig. 10; LAMEERE, 1917, Mus. Nat. Hist. Natur., Bull., vol. 23, p. 145; HANDLIRSCH, 1919, Denkschr. Akad. Wiss., vol. 96, p. 67, fig. 75; HANDLIRSCH, 1920, in Schröder's Handbuch, vol. 3, p. 171, fig. 127.
Corydaloides brongniarti HANDLIRSCH, 1919, Denkschr. Akad. Wiss., vol. 96, p. 68, fig. 76.
Corydaloides longipennis HANDLIRSCH, 1919, Denkschr. Akad. Wiss., vol. 96, p. 68, fig. 77.
Corydaloides simplex BRONGNIART, 1894, Recherches Hist. Ins. Foss., pl. 16, fig. 8.
Corydaliodes simplex HANDLIRSCH, 1919, Denkschr. Akad. Wiss., vol. 96, p. 69, fig. 78.
Corydaliodes gracilior HANDLIRSCH, 1919, Denkschr. Akad. Wiss., vol. 96, p. 69, fig. 79.

This interesting and widely discussed insect was originally described from a single specimen (plate 16, fig. 6), though seven additional specimens were subsequently placed here by Brongniart. The preservation of these fossils is much poorer than the published drawings indicate. The type specimen already mentioned (16-6) is the best of the fossils in most respects; the half of the specimen shown in Brongniart's figure 6 is actually in three pieces and specimen 16-12 is the counterpart. Brongniart's fossil 16-7 (the type of Handlirsch's *brongniarti*), consisting of the fore wing and part of the hind, shows most clearly the venation of the fore wing. Specimen 16-9, the type of Handlirsch's *gracilior*, is now in such poor condition that the venation, antennae and head, all depicted by Brongniart, can no longer be discerned; assignment of this specimen even to any genus is uncertain. Specimen 16-10, the type of Handlirsch's *longipennis*, shows parts of both fore and hind wings, especially the distal part of the hind, though the wing has been slightly distorted and appears more slender than it probably was originally. Specimen 16-11, which Brongniart depicted as consisting of the abdomen and two small fragments of the wings, could not be found in the Museum collection; it might be the counterpart of specimen 16-10, but there is not enough of the insect to indicate even its generic or family position. Specimen 16-13, which I was unable to find in the collection, was depicted by Brongniart as consisting of parts of the body, but obviously had none of the wings preserved, so that its assignment even to the order Megasecoptera is dubious.

Since I am convinced, for reasons indicated below, that all of the above-mentioned specimens which can be referred to the Corydaloididae belong to one species (*scudderi*), I have used them as the basis of the following account of this insect:

Wings: The fore wing, complete, is 48 mm. long and 14 mm. wide in the type, and is approximately the same in other specimens. The hind wing has the same dimensions, but is broader proximally, and has a wider anal area. Although the convexities and concavities of the veins are not well indicated in any of the fossils, the homologies of the veins are clear. The subcosta, which is indistinct in most specimens, can be followed in 16-10 to the level of the fork of R2 and R3. The anastomosis between MA and Rs and between CuA and M is nearly the same in all specimens. Slight variation in the branching of the main veins occurs, but not more than is found in Megasecoptera in general. In the fore wing of specimen 16-6 Rs is apparently forked, though in the hind wing R3 is forked; in all other specimens, these veins are unbranched. The cross-veins between R2+3 and R1 are distinctly sigmoidal, but the others are straight. Although not so indicated in Brongniart's drawings, the cross-veins form three gradate series, as shown in the accompanying figure. In addition there are a few short cross-veins in the costal area. In none of the specimens are there indications of wing maculations or other marking.

Body: Little of the body of *scudderi* is actually known. The head is shown in four of Brongniart's figures, but three of the fossils represented (16-11, 16-9, 16-13) are so fragmentary or poorly preserved that their assignment even to the order Megasecoptera is questionable. Specimen 16-10 was depicted by Brongniart as including a small head, conspicuous eyes, and the bases of the antennae; but the fossil now seems to lack the head entirely, the rock fragment being broken along the prothorax. It seems to me, therefore, that nothing is actually known about the head of *scudderi*. The thorax is partially preserved in 16-6, which shows only its general form and part of a leg. I have been unable to see the prothoracic spines which Brongniart showed in his drawing of specimen 16-10; the fossil has either deteriorated or been broken since he studied it. Lameere has referred to the apparently five-segmented tarsus of specimen 16-13, but as noted above, I was unable to find the fossil in the Museum collection, and, on the basis of Brongniart's figure, I question its assignment to *Corydaloides* or even the family Corydaloididae.

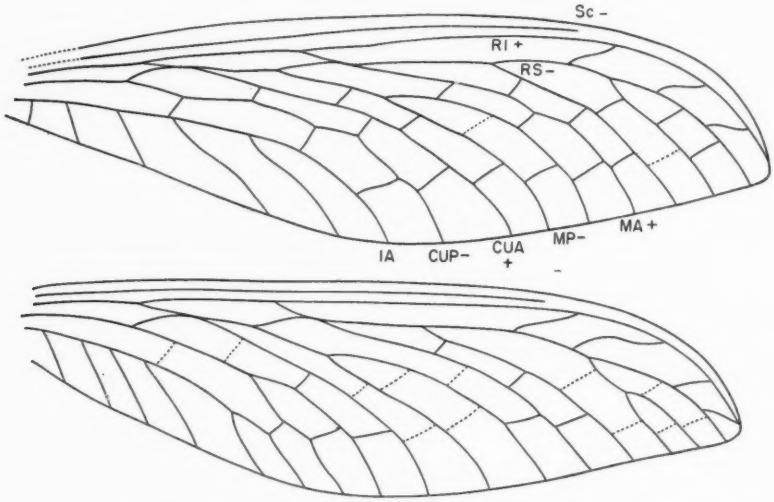


FIG. *10—Corydaloides scudderi* Brongniart. Drawing of fore and hind wings, based on all known specimens. Veins not preserved are represented by broken lines. Lettering as in figure *1*.

The abdominal structure of *scudderi* has been widely discussed in the literature. The abdomen is preserved, at least in part, in several specimens, especially 16-6 and 16-10 and it is 25 mm. long and 9 mm. wide (maximum). The bases of the cerci are discernible in 16-6. The only notable feature of the abdomen is the presence of paired lateral projections on all abdominal segments. These are shown in Brongniart's plates (16-6 and 16-10) and more diagrammatically in his text-figure 5. I agree entirely with Lameere that these projections are extensions of the tergites and that they do not show tracheae, as drawn by Brongniart. Each of the projections bears a pair of distal spines, not three as shown in Brongniart's drawing (text-fig. 5). As Lameere has pointed out, also, these lateral processes are apparently homologues of similar structures in the Palaeodictyoptera, such as *Stenodictya*, as well as in several Recent Ephemerida, as *Oniscigaster* and *Siphlonisca*.

Synonymy.[3]—*Corydaloides simplex* was based by Brongniart on a very poorly preserved and fragmentary specimen. Although the venation, as drawn by Brongniart, differs markedly from that of *scudderi*, the wings are so obscure that I believe that Brongniart's drawing is not reliable and I agree with Lameere that nothing shows in the fossil which separates it from *scudderi*. *C. brongniarti* was erected by Handlirsch for one of Brongniart's specimens (16-7), on the grounds that its radial sector had one more branch than that of Brongniart's type, 16-6. As I have pointed out above, however, this amount of variation is well within that which occurs in all Megasecoptera, or for that matter, most insects with a full venation. *C. longipennis* Handlirsch was established for Brongniart's specimen 16-10, which he thought had more slender wings than the type of *scudderi*; but it is apparent from the fossil that its wings have been wrinkled and distorted during preservation. *C. gracilior* Handlirsch was established on the poorly preserved fossil 16-9 and placed in his genus *Corydaliodes*. The condition of the specimen prevents any satisfactory conception of the venation, and though even its family position may be doubtful, I believe *gracilior* should be placed in synonymy with *scudderi*.

Handlirsch's restoration of *C. scudderi* (1921, p. 171, fig. 127) is highly imaginative and misleading. Not only does he show structures, such as the antennae, legs, eyes and cerci, of which we know nothing, but he has incorrectly represented the venation, especially that of the hind wing.

Affinities.—The Corydaloididae combine a number of generalized and specialized characteristics found elsewhere in the order. The relatively broad costal and subcostal spaces are generalized traits, also occurring in the sphecopterids and mischopterids. The nearly even distribution of cross-veins is suggestive of the Aspidothoracidae. On the other hand, the anastomosis of CuA and M as well as of Rs and MA is a specialization that is unknown in other Commentry Megasecoptera except for *Ischnoptilus*. The Corydaloididae appear to have been derivatives of the same group that gave rise to the mischopterids, before the acquisition of the serial cross-veins.

Family Foririidae

Systematic descriptions.—This family was established by Handlirsch in 1919 for the genus *Foriria* Meunier, from Commentry. As in the cases previously noted, Handlirsch knew the fossil only by Meunier's crude drawing. A revised diagnosis of the family being necessary, the following is proposed:

Wings: Hind wings broader and shorter than the fore, but with the same basic venation. Sc remote from the margin and terminating on R1 as in Sphecopteridae; costal and subcostal spaces about equal in width; stem of M close to R but not fused with it; MA free from Rs; stem of Cu very remote from M; CuA not diverging towards MP; one anal vein. Cross-veins close together and straight in costal and subcostal areas; the others strongly sigmoidal and arranged so as to form two rows.

Genus Foriria Meunier

Foriria Meunier, 1908, Mus. Nat. Hist. Natur., Bull., vol. 14, p. 172; Handlirsch, 1919, Denkschr. Akad. Wiss., vol. 96, p. 67; La-

[3] *C. gracilis* Brongniart (l. c., 1885, p. 64) is a nomen nudum.

MEERE, 1917, Mus. Nat. Hist. Natur., Bull., vol. 23, p. 144.

Wings: Rs arising just basad of mid-wing, with three terminal branches; all other veins unbranched; a long cross-vein between R2+3 and R1 in the fore wing, but not in the hind; 1A short, extending only to the level of the origin of Rs. Maculations on both wings.

Genotype: Foriria maculata Meunier.

R2+3 is forked, R2 reaching the apex of the wing. A long sigmoidal cross-vein extends from R2+3 to R1, and there are two cross-veins between all main veins, with an additional one between R2+3 and R4+5, and R1 and R2+3.

The hind wing is 30 mm. long and 10 mm. wide (maximum), and is broadest in the region of the end of 1A. The venation is like that of the fore wing except for an

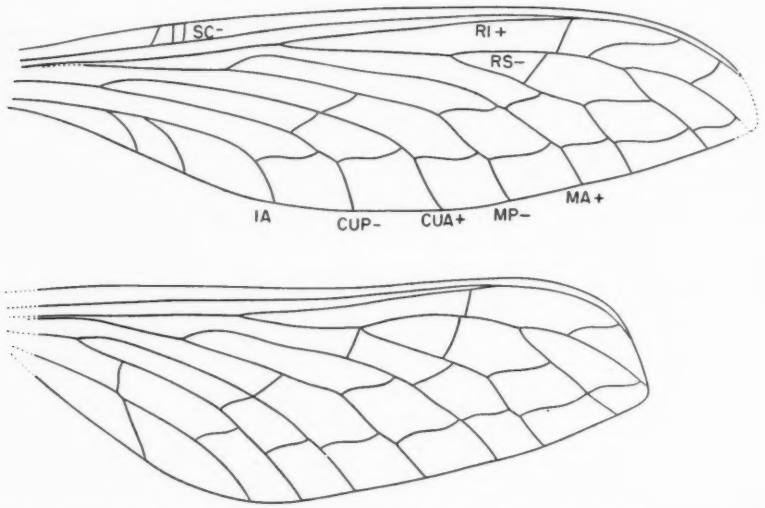


FIG. *11—Foriria maculata* Meunier. Fore and hind wings of type. Lettering as in figure *1*.

FORIRIA MACULATA Meunier
Figure 11

Foriria maculata MEUNIER, 1908, Mus. Nat. Hist. Natur., Bull., vol. 14, p. 172; MEUNIER, 1909, Ann. Paleont., vol. 4, p. 140, fig. 11, pl. 1, fig. 6; LAMEERE, 1917, Mus. Nat. Hist. Natur., Bull., vol. 23, p. 144; HANDLIRSCH 1919, Denkschr. Akad. Wiss., vol. 96, p. 67.

This species is known by two specimens, both types. One of these, figured by Meunier, consists of a complete fore wing and a nearly complete hind wing; the other specimen, which was not illustrated by Meunier, shows the four outstretched wings and part of the thorax. The following account is based on these two fossils.

Wings: The fore wing is 35 mm. long (not 50 mm., as stated by Meunier) as preserved, and 9 mm. wide; the entire length was probably around 38 mm. The wing is narrowed proximally, but is not truly petiolate.

extra cross-vein between CuP and 1A, and that between Rs and MA; and the absence of the long cross-vein between R1 and R2+3. Both fore and hind wings are traversed by light bands, with two apical spots resembling those of *Sphecoptera*.

Body: The type specimen not figured by Meunier shows the pterothorax and apparently part of the prothorax. The latter appears to be much like that of *Aspidothorax*, as pointed out by Lameere. The spines that Lameere thought were attached to the fore leg appear to me to be part of prothorax. There is no doubt, however, that part of a fore leg is preserved, though I am unable to discover the tarsal segmentation. The leg structure resembles that of *Aspidothorax*, more than that of *Mischoptera*.

Affinities.—The Foririidae, though in-

completely known, appear to be derivatives of the ancestral stock of the Mischopteridae. This is indicated by the serial arrangement of the sigmoidal cross-veins and the relatively broad costal and subcostal spaces. The absence of anastomosis of Rs and MA, however, indicates a more generalized stock than the Mischopteridae, while the distinct termination of Sc on R1 is suggestive of the sphecopterids. The most striking feature of the foririid wings, the differentiation of the two pair, is unique among the known Carboniferous Megasecoptera.

INSECTA INCERTAE SEDIS

Insectorum gen. indet. *pulchra* Brongniart

Sphecoptera pulchra BRONGNIART, 1894, Recherches Hist. Ins. Foss., p. 295, pl. 17, fig. 1; HANDLIRSCH, 1908, Foss. Ins., p. 319, pl. 33, fig. 10.

The type of this species consists of a small fragment of a wing which was obviously much larger than that of known sphecopterids. Since very little of the insect is known, even its ordinal affinities are uncertain.

SUMMARY

Study of the Megasecoptera of the Commentry Basin shows that:

(1) Fourteen species, assigned to six families and 11 genera are recognizable.

(2) These species represent several lines of evolution within the strictly palaeopterous line. The changes involved in the evolution of these families include: (a) the anastomosis of Rs and MA, followed by (b) the anastomosis of MP and CuA; (c) the crowding of the anterior veins along the costal margin; (d) serial arrangement of cross-veins, with reduction in their total number and in the number of rows.

(3) The genus *Cyclocelis*, in recent years treated as a synonym of *Sphecoptera*, is distinct and valid.

(4) The genera *Sphecoptera* and *Cyclocelis* formerly placed in the Mischopteridae, require separation into a distinct family, the Sphecopteridae.

(5) The genus *Ischnoptilus*, formerly placed in the Mischopteridae, also requires separation into a new family, Ischnoptilidae.

MANUSCRIPT RECEIVED JULY 28, 1950.

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PHOSPHORIA CONODONTS FROM SOUTHEASTERN IDAHO

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ABSTRACT—Very little information is available in regard to Permian conodonts. Three small collections from the Phosphoria formation of southeastern Idaho provide the basis for the present report. The specimens are poorly preserved and the variety is not great. However, the genera *Gondolella*, *Prioniodus?* and *Streptognathodus* are represented. Three new species are established—two of them belong in *Gondolella*, the dominant genus in the collections, and one in *Streptognathodus*. Because of the general lack of other described Permian conodonts, no precise correlations of the Phosphoria can be suggested on the basis of these fossils alone. However, their evolutionary stage, together with the associated faunas, including the edestid shark *Helicoprion*, suggest a Middle Permian age for the formation.

DURING the summer of 1949, a study was made of certain of the Paleozoic formations of Idaho south of the Snake River Plain. Special consideration was given to the possible microfossil content of these strata. The Phosphoria formation was sampled at several localities in the Caribou, Bear River, and Preuss ranges. Conodonts were secured at two localities in the Preuss Range and at a single locality in the Bear River Range. Altogether, more than 100 specimens were collected, many of which are only fragments. These conodonts are not well preserved and their variety is not great. Fifteen specimens, which represent the more nearly complete individuals, as well as the several genera and species which occur in the collections, are illustrated and described.

DISTRIBUTION OF PERMIAN CONODONTS

To date, no conodont faunas as such have been described from the Permian strata in any part of the world. That is, our present knowledge of Permian conodonts consists of a small number of isolated references to single or, at the most, a few individuals from Europe and the United States. Branson and Mehl (1941, p. 191) reported some specimens which were stated to have been collected from the Triassic Muschelkalk of Germany, but those authors suggest that the conodonts were perhaps derived from the underlying Pennsylvanian or Permian rocks; and later, Branson and Branson (1941, p. 133) concluded that the specimens "probably came from the lithologically similar Zechstein." In the United States, a few Permian conodonts have been reported from Nebraska, Kansas, Texas, and Wyoming (see, for example, C. C. Branson, 1932; Ellison, 1938, 1941; Kellett, 1943).

In addition, it should be added that Permian conodonts in considerable abundance were recently found by H. R. Downs in the Bennett shale of Kansas, and they are the basis for a report now in preparation by Miller, Downs, and Youngquist. Also, not long ago, R. M. Jeffords told us orally that he had secured some conodonts from the Lower Permian Hughes Creek shale north of St. Marys, Kansas.

At the present time, it is generally agreed that the known geologic range of conodonts is from the Lower Ordovician into (but not through) the Permian. Reports of Triassic and younger forms remain to be verified.[1] Of the several systems involved, the Permian has yielded by far the poorest conodont representation of any.

DISTRIBUTION OF CONODONTS IN WESTERN UNITED STATES

Although the study of conodonts had its origin in Europe, the greater portion of the literature at the present time is based on faunas from the United States. However, from a geographic (and to a considerable

[1] Since this manuscript was completed, the senior author has secured conodonts from the Triassic sediments of southeastern Idaho. For reasons which will be presented in a separate study of these forms, these conodonts are believed to be indigenous to the strata in which they were found. The range of the conodonts probably extends into the Triassic as was suggested by Eicher in 1946.

extent from a stratigraphic) point of view, conodonts are but poorly known even in this country. One of the areas here which has yielded remarkably few specimens, considering the amount of stratigraphic and paleontological work that has been done in the region, is the Appalachian Mountains. Only a few conodonts have been described from there, and these come principally from the southern portion of the area, that is, Alabama. However, another region in the United States of even greater magnitude has similarly yielded very few specimens. This area centers in the Basin and Range Province, but may be conveniently thought of as embracing the Rocky Mountain states of Montana, Wyoming, Colorado, New Mexico, and all states westward.

In Montana, conodonts have been described from the Heath formation in the western part of that state (Scott, 1934, 1942); from a "Lower Mississippian black shale" in central and western Montana (Cooper and Sloss, 1943); and from a Devonian black shale in the Flathead Range to the northwest (Cooper, 1945). In addition, they have been recorded, but not illustrated or described, from a black shale (possibly Mississippian), just above limestones assigned to the Three Forks formation, which crops out near Half Moon Pass in the Big Snowy Mountains (Deiss, 1936), and from the Kinderhook of the Little Rocky Mountains (Knechtel and Hass, 1938; Hass, 1943).

Conodonts in Wyoming have been described from the Upper Ordovician of the Bighorn Mountains by Amsden and Miller (1942). Specimens from the Phosphoria have been recorded by C. C. Branson (1932), and figured but not described from that formation by Branson and Mehl (1941). They have also been reported from the Mississippian and Pennsylvanian of Wyoming (Branson and Mehl, 1938); from the Tensleep and Phosphoria of the Wind River Mountains (Branson and Branson, 1941); from the Darby (Branson and Mehl, 1938); and from the Hartville along the east side of the Laramie Range at Guernsey Dam (Branson and Mehl, 1941).

Colorado, like Wyoming, to date has yielded only one described conodont fauna, and it is from the Ordovician Harding sandstone. The assemblage was first noted, and figured in part by Kirk (1929), and later was illustrated and described in some detail by Branson and Mehl (1933). Conodonts have been reported from the Pennsylvanian Paradox formation of western Colorado by Johnson (1945, p. 91). Along the east side of the Colorado Front Range an occurrence in the Pennsylvanian Glen Eyrie formation was recorded by McLaughlin (1947, pp. 1947, 1973, 1974).

No conodonts have been described from Utah, but Baker, Dane, and Reeside in 1933 incidentally noted that a number of specimens were found in a portion of the Pennsylvanian Paradox formation encountered during the drilling of an oil test in the eastern part of the state near Moab.

Conodonts do not seem to have been either described or recorded from New Mexico, and Dr. Alexander Stoyanow of the University of Arizona (personal communication dated May 22, 1948) has indicated that insofar as he is aware none are known from that state.

Nevada, California, Oregon, Washington, and Idaho to date have yielded no conodonts which have been described or recorded in print. However, through the extensive work of the United States Geological Survey on the phosphate deposits of Idaho and adjacent regions, it has been known for a number of years that at least a few forms occur in the Phosphoria formation of Idaho and Utah (as well as Wyoming).

The total lack of conodont literature based on faunas from New Mexico, Arizona, Nevada, California, Washington, Oregon, and Idaho is readily apparent from the foregoing summary. The relatively numerous references to conodonts from Montana, Wyoming, and Colorado, would superficially seem to indicate that these fossils are well known from that general region. However, careful analysis of the literature shows that in only seven short papers (including Scott's two reports on assemblages) are specimens illustrated and described. The other references are indeed brief and consist for the most part of a single line or less which notes the presence of these fossils.

Although conodonts as a group have

been given relatively little study even in the United States, the paucity of information about their occurrence in the western portion of our country is striking and would seem to indicate a promising field for research. However, it appears to us, from recent experience in attempting to secure microfaunas from the Paleozoic rocks of southeastern Idaho, that the collecting of conodonts from western United States may require relatively more effort than in the Mid-Continent region. Part of the reason for the lack of conodont literature on western faunas can perhaps be ascribed to the reconnaissance nature of many of the studies in the region. However, the same can not be said for the Appalachian Mountains where careful study has been given to many of the microfaunas and to the detailed composition of the sedimentary rocks. A consideration of the ecology may yield a partial explanation of this problem.

The ecology of conodonts has been given only brief note, but Branson and Mehl (1934) have suggested that the conodont-bearing animals were particularly abundant in shallow water, which may have been brackish or possibly even fresh. These authors add that their collections have come mainly from shales, and that further collecting may prove conodonts to be abundant also in limestones. Insofar as our experiences are concerned, three facts appear to stand out with regard to the occurrence and associations:

1. Conodonts are commonly found in formations or in zones of formations which are almost completely lacking in other invertebrate fossils, both macro- and micro-.
2. Conodonts are commonly found associated with fragmental plant remains, and in stratigraphic units which represent marine but nearshore, lagoonal, or perhaps estuary deposits, with little regard to latitude.
3. Conodonts are commonly associated with fish remains, and their known geologic history, apparently confined to the Paleozoic (see footnote), parallels that of the Paleozoic fishes to a considerable extent. This may or may not be merely coincidental. However, both conodonts and fishes appear about the same time in the Ordovician; and the former probably reach their climax in diversity and abundance in the Upper Devonian and Lower Mississippian, when fishes also were abundant. Conodonts are relatively rare in the late Mississippian but reach a secondary climax in abundance (but not variety) approximately in the mid-portion of the Pennsylvanian, and there again are commonly associated with fish (as well as plant) remains in black shales.

In general, it seems that conodonts are most likely to be found associated with shallow water deposits, and that the sediments which accumulated in the relatively deeper portions of both the Appalachian and the Cordilleran geosynclines are not likely to contain many specimens. Conodont-bearing animals probably occurred more commonly along the shallower margins of these regions (e.g., western New York), or around shoal or island areas within deeper geosynclinal waters. Black shales are probably not indicative of any particular depth of water. Nevertheless, many of those in the Mid-Continent region are certainly suggestive of shallow water origin, and it is believed that the same observation may be applicable to at least some of the conodont-bearing black shales of the Rocky Mountain area.

PRESENT STUDY

During the summer of 1949 a field investigation was made of the late Paleozoic rocks of southeastern Idaho, and numerous samples were secured with the possibility in mind of ascertaining their microfossil content. The younger Paleozoic strata of the region include (in ascending order) the Madison, Brazer, Wells, and Phosphoria formations—a sequence attaining a thickness of more than 5,000 feet. The microfossils of these sediments have been given little consideration in the past, but present interest in subsurface exploration by drilling in this part of Idaho suggests that microfossils may be of increasing importance in the near future. Some of the samples secured from the Phosphoria formation yielded conodonts, and they are the basis for the present report.

These conodonts came from three localities (and five horizons) in southeastern Idaho, as follows:

1. San Francisco Chemical Company workings, east side of U. S. Highway 89, NE ¼ sec. 6, T. 13 S., R. 45 E., Bear Lake County, Idaho (locality based on Montpelier, Idaho-Wyoming-Utah quadrangle), in black shale about 6 inches below "cap rock"—lower Phosphoria.

2. Locality same as 1 but from brown shale about 2 feet below "cap rock"—lower Phosphoria.

3. West side of U. S. Highway 89, SW ¼ sec. 31, T. 12 S., R. 45 E., Bear Lake County Idaho, about 10–20 feet above Wells formation—lower Phosphoria.

4. Northeast side of Paris Canyon, about ½ mile northeast of old abandoned phosphate plant, NW ¼ sec. 9, T. 14 S., R. 43 E., Bear Lake County, Idaho—composite sample from 50 feet of the formation just below the Rex Chert member (which is the uppermost unit of the Phosphoria).

5. Same locality as 4, but from about the mid-portion of the Phosphoria.

In the following text, each horizon is regarded as a locality.

PHOSPHORIA CONODONTS AND ASSOCIATED FOSSILS

Altogether about 100 conodonts (or fragments apparently representing more than half of an individual) were collected. The specimens seem to be fresh and unaltered by any weathering, and it is believed that they have not been reworked from older strata but are indigenous to the Phosphoria. However, in general, the material is difficult to study for the phosphatic shales were not easy to wash, and many of the individuals were broken during the process. In addition, the phosphatic shale matrix did not part readily from the conodonts and the well-known technique of cleaning these fossils by means of glacial acetic acid was not effective. The conodonts secured from the Paris Canyon localities appear to be the most satisfactory with which to work, for they came from a shale zone which is relatively low in phosphate content. They washed out cleanly, but were, however, also broken in the process.

The conodonts described from the Phosphoria formation in this report are:

Gondolella idahoensis Y., H., & M., n. sp.
G. phosphoriensis Y., H., & M., n. sp.
G. spp.
Prioniodus? spp.
Streptognathodus sulcoplicatus Y., H., & M., n. sp.

Although our collections are numerically rather small (about 100 specimens), when they are compared with older faunas, some marked differences are apparent both in general composition and in the details of the assemblage.

This is the youngest conodont fauna so far described, and certain evolutionary trends which are not readily apparent in Pennsylvanian forms seem fairly clear when viewed in the light of this Permian assemblage. The predominance of representatives of *Gondolella* in our collections, and the relatively few other genera present are noteworthy. Also, the Phosphoria conodonts are in general small in comparison to some of the strikingly large idiognathids, streptognathids, and gondolellids found in Middle and late Pennsylvanian strata. The apparent total absence of representatives of *Hindeodella*, which are very abundant in many Pennsylvanian assemblages, is also worthy of comment. The absence of this genus may be a matter of collecting, but *Hindeodella* must be at least materially reduced in numbers in this Phosphoria fauna for it does not occur in any of the numerous samples examined.

Species of *Gondolella*, numerically the largest single generic element in the assemblage, seem to exhibit some distinct evolutionary trends when compared with their older congeneric relatives. The oral platform surface tends to be smooth rather than rugose, and in particular the height of the denticles which form the median ridge is materially less on these Permian specimens. Pennsylvanian forms commonly bear distinctly elongate denticles forming a comb-like structure (particularly anteriad); but this median ridge in the Phosphoria specimens is low and is composed of nodes (sometimes fused to form a low ridge), and the anterior portions of only a few specimens show nodes sufficiently

elongate to be regarded as denticles.

In general, the Phosphoria conodonts show a reduction in size, diversity, ornamentation, and (in our experience) abundance, when compared to Pennsylvanian faunas. C. C. Branson (1932) states that some beds of the Phosphoria formation in Wyoming "are rich in shark and conodont remains." In Idaho at least, our collecting indicates that conodonts are relatively rare in the Phosphoria. Dr. W. H. Hass of the United States National Museum has indicated by letter that his collections from the Phosphoria of this region are likewise limited.

The specific beds in which the conodonts were found seemed to contain no other fossils. However, stratigraphically within a few feet of the conodont-bearing shales in the lower Phosphoria of our localities 1 and 2, a variety of other marine forms occur. These include brachiopods in considerable abundance, pelecypods, gastropods, and possibly some scaphopods. The well known gastropod *Omphalotrochus ferrieri* occurs in great abundance in beds just a few feet higher than those which yielded the conodonts at our localities 1 and 2 in Montpelier Canyon. Considerable time was spent in this canyon in search of cephalopods; two nautiloids were found, one of which belongs in *Mooreoceras*, whereas the other is referable to *Stearoceras*. The latter form is close to and may be conspecific with *S. phosphoriense* (Branson) described first from the Phosphoria of the Owl Creek Mountains of Wyoming (C. C. Branson, 1930, p. 59). In addition, nine specimens of the unusual Permian edestid shark *Helicoprion*, were collected.

SIGNIFICANCE OF THE FAUNA

The age of the Phosphoria has been the subject of intermittent discussion ever since the formation was first described and named by Richards and Mansfield (1912, pp. 683–689) from Phosphoria Gulch in northern Bear Lake County, Idaho. Various groups of fossils have been used to date the formation (C. C. Branson, 1930). In 1934, Miller and Cline (p. 281) on the basis of a few ammonoids from one horizon in the Phosphoria of westernmost Wyoming, placed the containing beds in the Middle Permian and stated that they are probably correlative with the Word of Texas. From fusulinid evidence in the Phosphoria of Montana, Frenzel and Mundorff (1942) regarded the basal Phosphoria as Lower Permian and correlated it with the Wolfcamp and Hueco of Texas. Recently, Newell (1948, p. 1054) has written that "paleontological evidence, although not yet summarized and not conclusive, suggests that both the Phosphoria and Kaibab faunas belong to the Word series of the standard Texas sequence." Inasmuch as there is no other described Permian conodont fauna with which to compare the present assemblage, the conodonts do not give any precise information on this age problem. In general, however, they appear to be appreciably younger than those known from the Upper Pennsylvanian (Virgil) of the Mid-Continent region, and they are also distinctly younger than those which occur in a fauna, now being described in manuscript, from the Bennett shale (near the base of the Lower Permian) of Kansas.

The incidental discovery of the nine

EXPLANATION OF PLATE 54

All specimens illustrated on this plate are from the Phosphoria formation at five localities in southeastern Idaho. The drawings are approximately ×50.

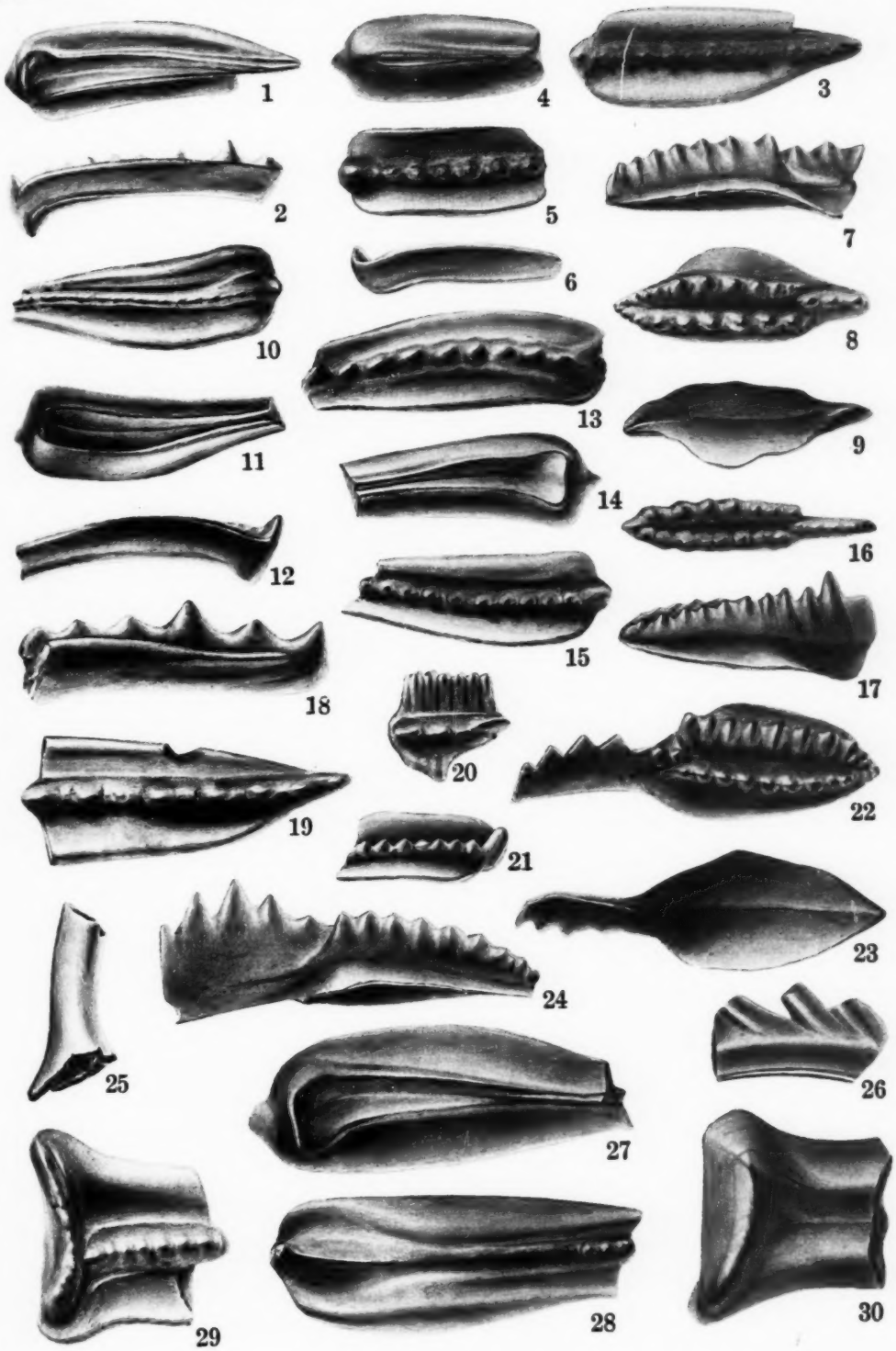
FIGS. *1–3, 14, 15—Gondolella idahoensis* Y., H., & M., n. sp. Three views of the holotype (figs. *1–3*), and aboral and oral views of a paratype. (p. 361)

4–6, 13, 18–21, 29, 30—Gondolella spp. Six fragmentary specimens. Figs. *4–6* represent one individual, as do fig. *13*, figs. *18*, *19*, fig. *20*, fig. *21*, and figs. *29*, *30*, respectively. (p. 362)

7–9, 16, 17, 22–24—Streptognathodus sulcoplicatus Y., H., & M., n. sp. Figs. *22–24* represent the holotype; and two fragmentary paratypes are shown by figs. *7–9*, and *16*, *17*, respectively. (p. 363)

10–12, 27, 28—Gondolella phosphoriensis Y., H., & M., n. sp. Three views of the holotype (figs. *10–12*), and two of a large paratype (figs. *27*, *28*). (p. 362)

25, 26—Prioniodus? spp. A fragmentary cusp, and a section of a denticulate bar, both of uncertain affinities. (p. 363)



Miller, Hawley, Youngquist, Phosphoria conodonts

specimens of *Helicoprion* in the lower Phosphoria during investigations for the present study offers an additional suggestion with regard to the age of the containing beds. It should be noted that James Steele Williams and others have also secured a few specimens of a "*Helicoprion*-like" form from the phosphatic shales of the Phosphoria in Utah and Idaho (Williams and Dunkle, 1948). Wheeler (1939) presented a comprehensive summary of the world-wide occurrence of *Helicoprion* and related forms and concluded (p. 105) that "the *Helicoprion* biozone does not extend below the *Omphalotrochus* zone of the Uralian stage, nor above the top of the Artinskian." Teichert's paper on *Helicoprion* from Australia (1940) indicates that he likewise regards the genus as being limited to the Uralian and Artinskian, and incidentally notes that in America "one specimen of *Helicoprion* occurs in the Artinskian Phosphoria formation"—the Artinskian is generally regarded as about Leonard in age.

SUMMARY AND CONCLUSIONS

Permian conodonts are very little known. About 100 specimens from the Phosphoria formation of southeastern Idaho provide the basis for this report, which is relatively the largest treatment of Permian conodonts to date. It is believed that these specimens are indigenous to the Phosphoria and were not derived from older strata. However, due to their small and fragile nature, they were considerably broken during our washing process, especially because the phosphatic shale matrix makes clean separation difficult. The genus *Gondolella* is by far the dominant element, but *Streptognathodus* and probably *Prioniodus* are also represented.

The almost total lack of other described Permian conodonts precludes any precise correlation with well established stratigraphic sections, but the general aspect of this Phosphoria assemblage indicates that it probably belongs somewhere in the Middle Permian. Nine representatives of the edestid shark, *Helicoprion*, collected from the Phosphoria during the progress of field investigations, are compatible with this age-determination.

ACKNOWLEDGMENTS

The preparation of this report has been made possible by a grant from the University of Idaho Research Fund through Special Research Project 23, and is one of a series of studies of the stratigraphy and paleontology of the late Paleozoic rocks of southern Idaho. Dr. R. M. Jeffords of the United States Geological Survey has orally contributed supplementary information on the presence of conodonts in the Permian of Kansas; Dr. W. H. Hass of the United States National Museum has given informative comments on the occurrence of conodonts in the Phosphoria of Idaho; and Dr. Alexander Stoyanow of the University of Arizona has written in regard to the apparent lack of known conodonts in that state. The illustrations which accompany the report were prepared by Mr. Howard Webster of Iowa City, Iowa. All of the type and figured specimens are in the Geology Department of the University of Idaho.

SYSTEMATIC PALEONTOLOGY

GONDOLELLA IDAHOENSIS Y., H., & M., n. sp.

Plate 54, figures 1–3, 14, 15

Oral surface of platform smooth and moderately concave. Carina consists of about ten to 12 discrete nodes; these are for the most part low, but the anterior two or three are elongate to the extent that they might be termed denticles. The posterior cusp is short and stout. On the aboral side, the escutcheon (and its accompanying flanges) is moderately expanded and is also attenuate in an aborad direction posteriorly (see pl. 54, fig. 2), but anteriorly it is narrow and elongate and is largely displaced by a short keel which is the anterior aboral termination of the specimen. The escutcheon continues onto the keel as a faint groove. Entire specimen gently arched and bowed.

This form is the most abundant species in our collections and probably represents a rather generalized type of *Gondolella* for conodont faunas of this age.

Occurrence.—Phosphoria formation at our locality 1 (figs. 1–3) and locality 2 (figs. 14, 15).

Types.—Univ. of Idaho, 800 (holotype, figs. 1–3) and 801 (figs. 14, 15).

GONDOLELLA PHOSPHORIENSIS Y., H., & M., n. sp.
Plate 54, figures 10–12, 27, 28

Platform gently bowed and arched. Lateral zones of platform smooth and thickened, but separated from carina anteriorly by narrow rather deep grooves; posteriorly the grooves are laterally expanded at the expense of the thickened platform margins. The carina is composed of low small discrete nodes in the anterior portion, but posteriad the nodes are subdued and are fused into a low ridge which is gently crenulate and which fuses posteriorly with the short stout posterior cusp. Aborally, the escutcheon is bounded by distinct flanges. Anteriorly the escutcheon is very narrow, though somewhat expanded posteriad. The extreme anterior end of the holotype (pl. 54, figs. 10–12) is missing, but the morphology of the preserved portion suggests that it was terminated anteriorly on the aboral side by a small keel which was narrowly grooved (extension of the escutcheon), and the carina on the oral surface was probably low and discretely nodose. This species differs from *G. idahoensis* in that the lateral zones of the platform are thickened, and the posterior portion of the carina is ridge-like rather than discretely nodose.

The specimen listed as *Gondolella* sp. from the upper Phosphoria of Wyoming and illustrated by Branson and Mehl (1941, pl. 7, fig. 8) appears to have a ridge-like carina in its posterior portion, and somewhat thickened lateral zones on the platform. It may be close to or conspecific with the form just described.

Occurrence.—Phosphoria formation at our locality 4 (figs. 10–12) and locality 1 (figs. 27, 28).

Types.—Univ. of Idaho, 802 (holotype, figs. 10–12) and 803 (figs. 27, 28).

GONDOLELLA spp.
Plate 54, figures 4–6, 13, 18–21, 29, 30

About 90 specimens of *Gondolella* occur in the collections under consideration, but the great majority of them are very incomplete. A representative variety of these fragmentary individuals has been illustrated. These specimens seem in almost every case to represent unnamed species, but unfortunately they are not well enough preserved to serve as types. The relative smoothness of the oral surfaces of the platforms of nearly all the specimens (except pl. 54, fig. 20) differentiates them from all, or almost all, described Pennsylvanian forms, the only specifically identified representatives of *Gondolella* available for comparisons. Figure 20 on plate 54 represents a very fragmentary specimen but was included because it is the only individual of the 90 which exhibits a rugose oral platform surface, reminiscent of Pennsylvanian species. Figures 4–6 on the same plate represent a specimen which has a smooth oral surface except for a very low relatively stout sinuous median nodose ridge, terminating posteriorly in a short stout cusp which is flattened distally. The escutcheon is very small, and is markedly elongate in proportion to its width. The specimen shown in inner oblique view by figure 13 on our plate has a carina which is composed of relatively discrete and sharply pointed nodes, and this carina terminates posteriorly in a cusp (partially preserved). The platform is slightly arched and bowed, and aborally it bears an elongate escutcheon much like that shown for example by the specimen illustrated by figure 14 on the same plate (though not as broadly expanded posteriorly). Figures 18 and 19 on this plate represent the anterior portion of a specimen which has a deeply grooved platform and large pointed but not particularly high denticles. Aborally, the anterior-most portion of the platform is produced into a keel, but the narrow escutcheon persists throughout the entire length of the preserved portion of this individual, continuing as a slight groove to the very end of the keel. Figure 21 is believed to represent approximately the posterior half of a specimen with a shallow smooth platform surface which bears a small spinose carina that terminates in a small rounded blunt cusp. Aborally, the escutcheon is narrow and deep, and it is set aside from the aboral platform surface by narrow sharp ridges. Posteriorly beneath the cusp, the escutcheon is slightly flared, and its posterior margin is projected a short distance aborad. Figures

29 and 30 illustrate a specimen which is unique in our collections in that it was probably the largest *Gondolella* in the assemblage (before it was broken). Also, it terminates posteriorly in a blunt laterally elongate process which orally bears an anteriorly bowed nodose ridge with no distinct cusp. The carina is stout and also nodose, and the oral platform surface is moderately concave and is smooth. The nature of the preserved portion of the escutcheon is well shown by figure 30. A series of faint contour-like ridges are also exhibited in this view, and these are presumed to be growth lines. The posterior termination of this specimen is somewhat like that of *G. neolobata* Ellison (1941, pl. 21, figs. 28, 32) for it bears a laterally expanded zone and transverse ridge. However, the Pennsylvanian form has a pronounced posterior cusp and a rugose surface on the oral side of the platform, in contrast to the Permian specimen.

Occurrence.—All figured specimens are from the Phosphoria formation at our locality 4. An unfigured fragment came from locality 3.

Repository.—Univ. of Idaho, 804 (figs. 4-6), 805 (fig. 13), 806 (figs. 18, 19), 807 (fig. 20), 808 (fig. 21), and 809 (figs. 29, 30).

PRIONIODUS? spp.
Plate 54, figures 25, 26

Two small fragmentary individuals in the collections we are studying indicate the probable presence of *Prioniodus*. Figure 25 represents a cusp (and short anticusp) which is expanded laterally along its base on the inner (figured) side to encompass a fairly large but apparently shallow escutcheon. The specimen represented by figure 26 appears to be a portion of a bar which is ovate in cross-section but flattened on its aboral surface. The denticles are strongly inclined posteriad and are apparently not in an alternating series as is characteristic of *Hindeodella*. Because of the fragmentary nature of the specimens, detailed descriptions are not feasible.

Occurrence.—Phosphoria formation at our locality 5 (fig. 25) and locality 4 (fig. 26).

Repository.—Univ. of Idaho 810 (fig. 25) and 811 (fig. 26).

STREPTOGNATHODUS SULCOPLICATUS
Y., H., & M., n. sp.
Plate 54, figures 7–9, 16, 17, 22–24

Platform high, almost straight, narrowly and deeply grooved on the oral surface. Lateral zones of oral surface marked by about eight to ten short stout transverse ridges which persist to but not across the deep median groove. The oral edges of the platform are prominently crenulated by these ridges. The blade is short and high and is composed of about five or six denticles, the central three of which are the largest. Anterior margin of blade appears to terminate in almost a right angle (see fig. 24, in which anterior-aboral corner of blade is missing). No carina is present—that is, the trend of the blade does not continue onto the platform by means of a carinal extension. Aborally, the platform margins are markedly flared to encompass the large escutcheon (see figs. 9 and 23—the flanges encompassing the escutcheon have been almost entirely broken away on the specimen represented by figs. 16, 17). No Permian specimens of this general age are available for comparison. The individuals under consideration differ from the considerably older late Pennsylvanian forms in that the present species has a narrower and more deeply grooved oral platform surface, the blade is shorter than is that of most other congeneric forms, and there is no carina on the platform (and no lateral nodes). There is a low short carina and at least a few small lateral nodes on the platforms of most Pennsylvanian representatives of this genus.

Occurrence.—Phosphoria formation at our locality 1 (all specimens).

Types.—Univ. of Idaho, 812 (holotype, figs. 22–24), 813 (figs. 7–9), and 814 (figs. 16, 17).

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JOURNAL OF PALEONTOLOGY, VOL. 25, NO. 3, PP. 365–371, PL. 55, 1 TEXT FIG., MAY 1951

MARCASITE FAUNA IN THE LUDLOWVILLE FORMATION OF WESTERN NEW YORK

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ABSTRACT—A remarkable faunal assemblage with an unusual mode of preservation occurs in the Ludlowville formation of western New York. The fossils are found preserved within marcasite concretions, the fossils themselves being either wholly or partly replaced by marcasite. These concretions form a clearly defined horizon marker within the upper part of the Ledyard shale member, traceable from Lake Erie to east of East Bethany, N. Y., a distance of 50 miles. This paper is concerned only with the fauna occurring within the concretions and an explanation is offered as to the conditions which brought about this sedimentary feature.

INTRODUCTION

PREVIOUS workers on the Hamilton group of western New York, A. W. Grabau (1896, 1898), H. F. Cleland (1903), and D. D. Luther (1906, 1914) make no mention of these concretions in their areal and paleontologic investigations while G. A. Cooper (1930) cites only the occurrence of "pyrite" concretions on Cazenovia and Avery Creeks, near Buffalo, N. Y. In addition to these two localities, the author examined the marcasite zone on Spring Creek, ½ mile northeast of Alden, N. Y., Erie County; Murder Creek, 1 mile north of Darien, N. Y., Genesee County; and exposures 2 miles west and 1 mile east of East Bethany, N. Y., Genesee County. Examination of the sections farther to the east failed to disclose the existence of the marcasite horizon. Save for the occurrence at Spring Creek, near Alden, N. Y., the exposures furnished only badly weathered concretions which crumbled readily due to oxidation of the iron sulfide. All of the species illustrated in this paper were collected from Spring Creek where a vertical shale bank and a horizontal exposure of the horizon in the stream bed furnished excellent material, considering the type of replacement.

The marcasitized fossils were released from the concretions only with extreme difficulty. The most advantageous method utilized was that of roasting the concretions on a hot plate and then immersing in cold water. The sudden change of temperature was sufficient to release the fossil from the matrix after which striking the concretion sharply with a hammer allowed the specimen to fall free in its entirety. In view of the fact that the marcasite oxidizes relatively rapidly, the fossils, after removal, were coated with a thin layer of shellac to inhibit oxidation.

The author has drawn freely from G. Arthur Cooper's Ph.D. thesis on the Hamilton group of New York. Considerable variance exists between certain of Dr. Cooper's measured stratigraphic sections and those of the author. Accordingly, his sections were modified so as to illustrate the field evidence. Grateful appreciation is extended to Dr. Rousseau H. Flower of the New York State Museum for assisting in the identification of the cephalopods and to Professor Edward S. C. Smith, Department of Geology, Union College for reading the manuscript.

STRATIGRAPHY AND PALEONTOLOGY

The Ledyard shale member of the Ludlowville formation, as defined by G. A. Cooper (1930), is a soft argillaceous shale, brownish gray or dark gray on the fresh surface but weathering light gray. It immediately overlies the Centerfield limestone and is delimited at the top, from Lake Erie to the Genesee Valley, by a thin bed of limestone termed the "*Strophalosia* bed," because of the abundance of the brachiopod *Strophalosia truncata*. To the east of the Genesee Valley, however, the *Pleurodictyum* zone of the Spring Brook shale member (Wanakah shale of authors) directly overlies the Ledyard shale. Constituting the "Third Leiorhynchus zone"

FIG. 1.—West-east cross section of Ledyard shale from Lake Erie to Canandaigua Lake, a distance of 85 miles, showing trough of sedimentation centering around Cazenovia Creek.

of Cleland (1903), the Ledyard shale is 60 feet thick on Paines Creek, Ledyard Township, Cayuga Lake (the type locality) and thins westward to 45 feet at Jaycox Run, Canandaigua Lake. The member then gradually thickens reaching a maximum of 80 feet along Cazenovia Creek at Springbrook, N. Y., 5 miles southeast of Buffalo, N. Y. The Ledyard shale then thins, over a distance of 9 miles, to 30 feet on Avery Creek, 3 miles south-southwest of Buffalo. In order to bring about the lagoon conditions to be discussed later, the author postulates the existence of a shoal, during Ledyard time, on the present site of Lake Erie which trended roughly northeast-southwest. The stratigraphic relations would seem to verify this (see text-figure 1).

While sedimentary marcasite and pyrite are present to a greater or less extent in virtually all sedimentary rocks, it is the black shales in which one commonly finds these minerals. It was therefore somewhat unusual to encounter a zone 2 inches thick replete with marcasite concretions occurring 27 feet above the base of the Ledyard gray shale. Few concretions were observed below this horizon and relatively few were found above the concretionary zone, the latter probably representing reworked material from the 2 inch zone. A thin bed of shaly limestone occurs from 5 to 20 feet above the marcasite layer, varying at each outcrop.

The shapes of the concretions are extremely varied, a few of the more common forms being shown on plate 55. Unexplainable is the fact that the elongated concretions seldom, if ever, contain enclosed fossils while the more nearly spherical ones virtually always possess a fossil as a nucleus. With a very few exceptions, all of the collected concretions show a pronounced radial structure. Most of the concretions exhibit a rough surface but about 10 per cent possess noticeably smooth exteriors. Occasionally sphalerite, galena, gypsum, calcite, or aragonite were found within the marcasite concretions, the minerals usually occurring as wholly or more often partly replaced marcasite fossils.

The present problem is the distinction between a truly dwarfed form and a normal immature form. Several criteria are utilized. According to Preston E. Cloud, Jr. (1948), "the beak features of the short hinged telotremate brachiopods are especially distinctive of relative age of growth. Immature shells are apt to show nearly straight beaks and delthyria only slightly modified by incipient deltidial plates. With increasing maturity, stronger curvature of the beak and fuller coverage of the delthyrium is attained." In cephalopods, closer spacing of the last several septa has long been recognized as proof of maturity with ornamentation a secondary criterion to be used with caution. The number and spacing of growth lines on a pelecypod are an indication of maturity. The most prominent lines are usually separated by others, less marked, their number and prominence being dependent largely on environmental conditions. It was found that a superior method of distinguishing dwarfs was a comparison of the fossils in question with the same species in adjacent formations where more favorable environmental conditions were suitable to normal growth.

It should be recalled that there are two main classifications of what are commonly referred to as "dwarf faunas." In one instance various organisms in their adult mature stage may be much smaller than the normal adult of the species due to a variety of circumstances inhibiting growth. In the other case some selective action has destroyed the larger forms leaving a diminutive but not a dwarfed fauna. Both conditions exist in this marcasite horizon, the latter case predominating.

It might be presumed that the sessile benthonic and the slowly moving vagrant benthonic forms would show the effects of dwarfing to a greater degree than the more mobile forms. This is partially borne out by the evidence encountered. The pelecypods are the most substantially affected and are true dwarfs in most cases. The brachiopods, which by reason of their sessile habit might conceivably be stunted, are apparently little affected and the majority of this group are normal mature, but diminutive forms. The single blastoid found was noticeably dwarfed. It is difficult to account for the fact that some of the cephalopods and gastropods are dwarfed since they could, of their own volition, leave the toxic environment for a more favorable one. That

they vary greatly in size, some exhibiting strong retardation while others are outwardly unaffected by the adverse environment, is proof that migration may have taken place. The trilobites are outwardly unaffected and are normal sized mature forms.

It is the author's supposition that the dwarfism of the forms under consideration is to be ascribed to physiological retardation of growth. This is in accord with F. B. Loomis' views on the "Tully Pyrite" (1903), a lens-like discontinuous bed of marcasite which occurs atop the Hamilton group in western New York and which erroneously has been correlated with the Tully limestone, whose stratigraphic horizon it occupies in western New York. A cursory examination by the writer reveals the fauna to be a truly Hamilton one.

A brief explanation of the paleoecology existent at the time of formation of the Ledyard marcasite horizon seems warranted in order to more clearly understand the problem at hand. Assuming that abnormal environmental conditions produced the diminutive forms, sedimentary analysis should reveal the dwarfing agent or agents and an areal investigation disclose the direction of infiltration of said agent or agents. The inhibitor in this case could be either the abnormally high concentration of H_2S or Fe or both since each alone is capable of producing dwarfing.* It is conceivable that the high percentage of iron could be introduced by normal weathering and transportation during Middle Devonian time. The Hamilton delta equivalents in eastern New York are predominantly red beds (Kiskatom) rich in iron, thereby indicating that this land mass possessed the available iron to contribute to the adjacent shallow seas. The author believes that the marcasite horizon indicates a temporary cutting off from the open sea accompanied by a greatly reduced influx of sediments or perhaps even a cessation of sedimentation. The concretions were then built up by precipitation of iron sulfide around the dead organisms as they lay on the muddy sea bottom, the animal itself undergoing replacement in stagnant water highly charged with hydrogen sulfide and iron. The prevailing lagoon conditions excluded oxygen-rich moving water, a prerequisite to normal growth. This landlocked body of water was probably analogous to the present day Black Sea. It is inferred that the relatively high concentration of H_2S was brought about by the decomposition of fecal material and plants.

* The writer has observed dwarfed individuals in the Furnaceville iron ore of Clinton age at Rochester, N. Y., where iron solely has been the stunting agent, the sulfur content being negligible.

EXPLANATION OF PLATE 55

All illustrations natural size unless otherwise designated.

FIGS. *1–3*—Some of the variable shapes of the marcasite nodules. Note the pronounced rough exteriors.

4—*Heliophyllum* sp. Marcasite concretion showing strong external similarity to a coral.

5—*Mucrospirifer* (*mucronatus*) Conrad ×1½, exceptionally well preserved pedicle valve.

6—*Ambocoelia umbonata* (Conrad) ×3.

7—*Chonetes lepidus* Hall.

8—*Loxonema hamiltoniae* Hall.

9—*Devonoblastus* sp. Calyx imbedded in nodule.

10—*Phacops rana* Green. Enrolled specimen imbedded in concretion.

11—*Hyolithes* sp. Note fine striations on surface of specimen and also the radial structure of the nodule.

12—*Bembexia sulcomarginata* (Conrad), ×2, apical view.

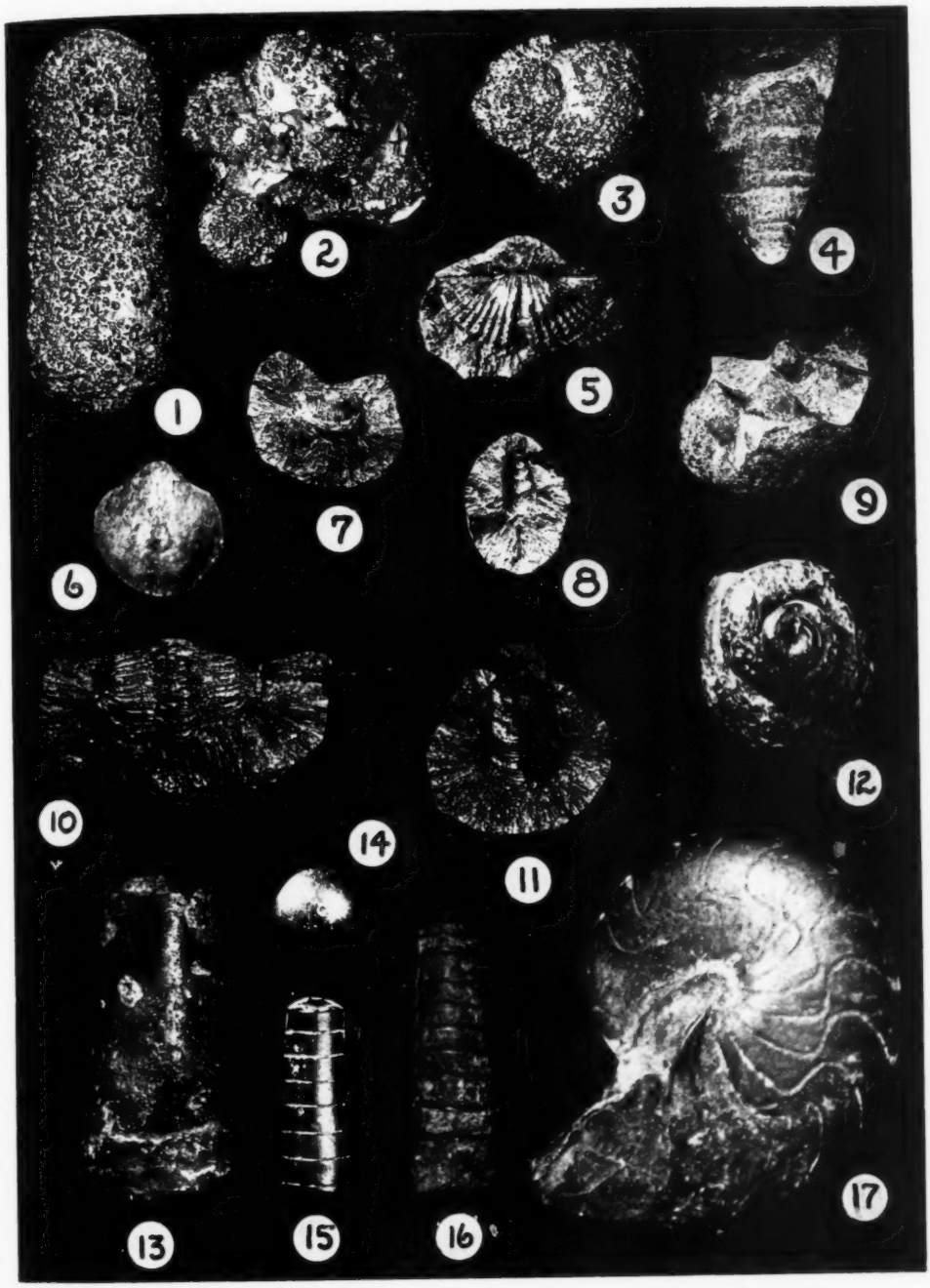
13—*Michelinoceras aldenense* Flower. External view showing constriction near aperture.

14—Apical view of same species showing position of siphuncle.

15—Phragmacone of same species.

16—*Spyroceras* sp.

17—*Tornoceras uniangulare* (Conrad), ×2. Excellent specimen denoting the character of the umbilicus and the simple goniatitic suture.



Fisher, Marcasite fauna in Ludlowville

An abnormally high amount of H_2S lowers the pH of the water and since this is a prime controlling factor in the development of organisms, both the size and quantity of individuals will be considerably reduced should the pH decrease. Furthermore an increase in the quantity of H_2S is invariably accompanied by a corresponding decrease in oxygen content. It is conceivable that a distinctly adverse environment may arise due to increased toxicity produced by excessive accumulation of decomposing material. An excess of excreta would lower the pH value and since the water is stagnant and not replenished by fresh oxygen-rich water, the environment would be extremely hostile to normal growth due to the decay of fecal material, dead organisms, and plants. It should be reiterated that this process is taking place in an inclosed basin containing a high concentration of population. Obviously, susceptibility to slight changes in toxicity varies with different animals. The accrued evidence

TABLE 1.—FAUNAL LIST OF THE LEDYARD SHALE MEMBER OF THE LUDLOWVILLE FORMATION IN WESTERN NEW YORK

L.—Ledyard shale
M.H.—Marcasite horizon
S.—Strophalosia limestone

	Grabau (1896)		Cooper (1930)		Fisher (1951)		
	L.	S.	L.	S.	L.	M.H.	S.
COELENTERATA							
Heliophyllum (?) sp.	—	—	—	—	—	r	—
BLASTOIDEA							
Devonoblastus sp.	—	—	—	—	—	rr	—
CRINOIDEA							
Stems and plates	r	—	—	—	—	—	—
BRYOZOA							
Species undetermined	—	—	—	—	—	—	rr
BRACHIOPODA							
Ambocoelia umbonata	rc	r	—	c	r	c	c
Athyris spiriferoides	—	—	—	—	—	rr	—
Brachyspirifer audaculus	—	—	—	—	—	rr	—
Chonetes lepidus	rc	—	c	—	rc	cc	—
C. mucronatus	r	—	—	—	rr	r	—
C. scitulus	r	—	—	—	—	—	—
C. setigerus	r	—	rc	—	r	rc	—
Leiorhynchus laura	c	—	cc	—	cc	—	—
Mucrospirifer mucronatus	rc	c	c	—	r	c	r
Nucleospira concinna	—	—	—	—	—	rr	—
Productella spinulicosta	r	—	—	—	—	r	—
Schuchertella arctostriata	r	—	—	—	—	—	—
Spinocyrtia granulosa	—	rr	—	—	—	—	—
Strophalosia truncata	r	cc	—	cc	—	—	cc
GASTROPODA							
Bembexia sulcomarginata	—	rc	—	—	—	rc	r
Bucanopsis leda	rr	cc	r	cc	rr	r	cc
Cyrtolites sp.	—	—	—	—	—	r	—
Diaphorostoma lineata	—	—	—	—	—	r	—
Loxonema delphicola	—	rc	—	—	—	r	rr
L. hamiltoniae	—	c	r	rc	—	cc	rc
Platyceras sp.	—	rr	r	—	—	—	—
Serpulospira laxus	rr	—	c	—	rr	rr	—

TABLE 1.—(*continued*)

	Grabau (1896)		Cooper (1930)		Fisher (1951)		
	L.	S.	L.	S.	L.	M.H.	S.
PELECYPODA							
Aviculopecten princeps	—	rr	—	—	—	—	—
Glyptocardia speciosa	—	rr	—	—	—	—	—
Grammysia arcuata	—	—	—	—	—	r	—
Modiella pygmaea	—	r	—	rc	—	r	r
Nucula corbuliformis	—	—	—	—	—	rc	—
Nuculites nyassa	—	—	—	—	—	rr	—
N. triqueter	r	—	—	r	r	c	—
Paleoneilo constricta	—	—	—	—	—	r	—
P. tenuistriata	—	rr	—	—	—	—	rr
Pterochaenia fragilis	c	—	c	—	c	cc	—
Tellinopsis subemarginata	—	rr	—	—	—	rr	—
CEPHALOPODA							
Bactrites sp.	—	—	—	—	—	r	—
Dolorthoceras sp.	—	c	—	—	—	—	—
Geisenoceras subulatum	—	—	—	rc	—	—	—
Michelinoceras aldenense	—	—	—	—	—	c	rr
Spyroceras sp.	—	—	—	rc	—	c	c
Tornoceras uniangulare	—	—	—	—	—	cc	—
Tornoceras n. sp.	—	—	—	—	—	rr	—
PTEROPODA							
Conularia sp.	—	—	—	—	—	rr	rr
Hyolithes sp.	—	—	—	—	—	c	—
Styliolina fissurella	c	—	rc	—	r	rr	—
Tentaculites gracilistriatus	c	—	—	—	—	—	—
TRILOBITA							
Dipleura dekayi	—	—	—	—	—	rr	—
Greenops boothi	r	rr	—	r	—	r	rr
Phacops rana	r	r	r	rc	rr	c	rc
OSTRACODA							
Primitiopsis punctulifera	r	—	r	r	r	c	r
PHYLLOCARIDA							
Echinocaris (?) sp.	—	—	—	—	—	r	—
PLANTS							
Species undetermined	—	—	—	—	—	rr	—

during this study demonstrates that pelecypods appear to be the least resistant to slight changes in pH and trilobites least impressible. The other groups exhibit varying intermediate degrees of susceptibility.

It seems probable that in the past, as today, marine invertebrates were extremely selective of water with favorable physical and chemical conditions for maximum metabolic activity. Numerous marine formations virtually barren of fossils attest to this fact.

While the marcasite horizon lies below the "*Strophalosia* bed" stratigraphically and therefore occurs within the Ledyard shale as defined by G. A. Cooper (1930), several notable faunal discrepancies were brought to light by this investigation. It is of interest to note that the fauna of the marcasite layer is a more prolific and varied one than that of the normal fauna of the Ledyard shale. In many respects the fauna shows no more affinity with the Ledyard shale than with the overlying Wanakah shale. Oddly enough, the brachiopod *Leiorhynchus laura*, the index fossil of the

Ledyard shale according to G. A. Cooper (1930), was not found within the marcasite concretions. Also, *Serpulospira laxus* supposedly is quite common in the Ledyard shale but only one specimen was found in the marcasite horizon. In contrast, the author was surprised to find the large development of cephalopods and gastropods, since it was presumed that the scarcity of these forms in the normal shale fauna would also persist in the marcasite layer. It is apparent that the ecological conditions postulated previously were conducive to the development of gastropods, as they thrive on excreta. This likewise applies to the multitude of pelecypods encountered, for this group comprises the most abundant class of organisms found within the marcasite nodules. More trilobites were found than had been anticipated from an examination of the literature, while the finding of unusual forms such as phyllocarids, conularids, a blastoid, fragmentary plant remains resembling *Lepidodendron*, and a very few corals was certainly not hoped for. The marcasite concretions are replete with the ammonite *Tornoceras uniangulare* which is unknown in the normal fauna of the Ledyard shale as well as in the Wanakah shale above. Considering that this is the earliest prolific occurrence of this form in New York state, this fossil is taken as the index of the marcasite horizon. Furthermore, this is the earliest horizon in which *Loxonema hamiltoniae*, *Michelinoceras aldenense*, and *Chonetes lepidus* are really abundant. Together with the brachiopod *Ambocoelia umbonata*, the ostracode *Primitiopsis punctulifera*, the abundant hyolithids, and the vast numbers of pelecypods, this faunal assemblage is markedly diagnostic of the marcasite horizon of the Ledyard shale in western New York.

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NEW SPECIES OF CRINOIDS FROM THE PENNSYLVANIAN OF KANSAS

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ABSTRACT—Six species from Pennsylvanian rocks of Kansas are described as *Sciadiocrinus humilis*, n. sp., *Erisocrinus lustrum*, n. sp., *Dicromyocrinus periodus*, n. sp., *Plaxocrinus gloukosensis*, n. sp., *Aesiocrinus tactilis*, n. sp. and *Lecythiocrinus tubiformis*, n. sp.

INTRODUCTION

IN THE fall of 1949, Richard Alexander (at present a student of geology at the University of Oklahoma), and the author collected crinoids at Melvern, Kansas from the Stull shale formation (Virgil series) and at Iola, Kansas from the Iola limestone formation (Missouri series). Three undescribed species were found in the Iola formation which, for the purpose of the present paper, are combined with two new species previously found by Allen Graffham in the Stull shale and Haskell formation (Virgil series) and a new form found several years ago by the author in the Iola formation at Coffeyville, Kansas.

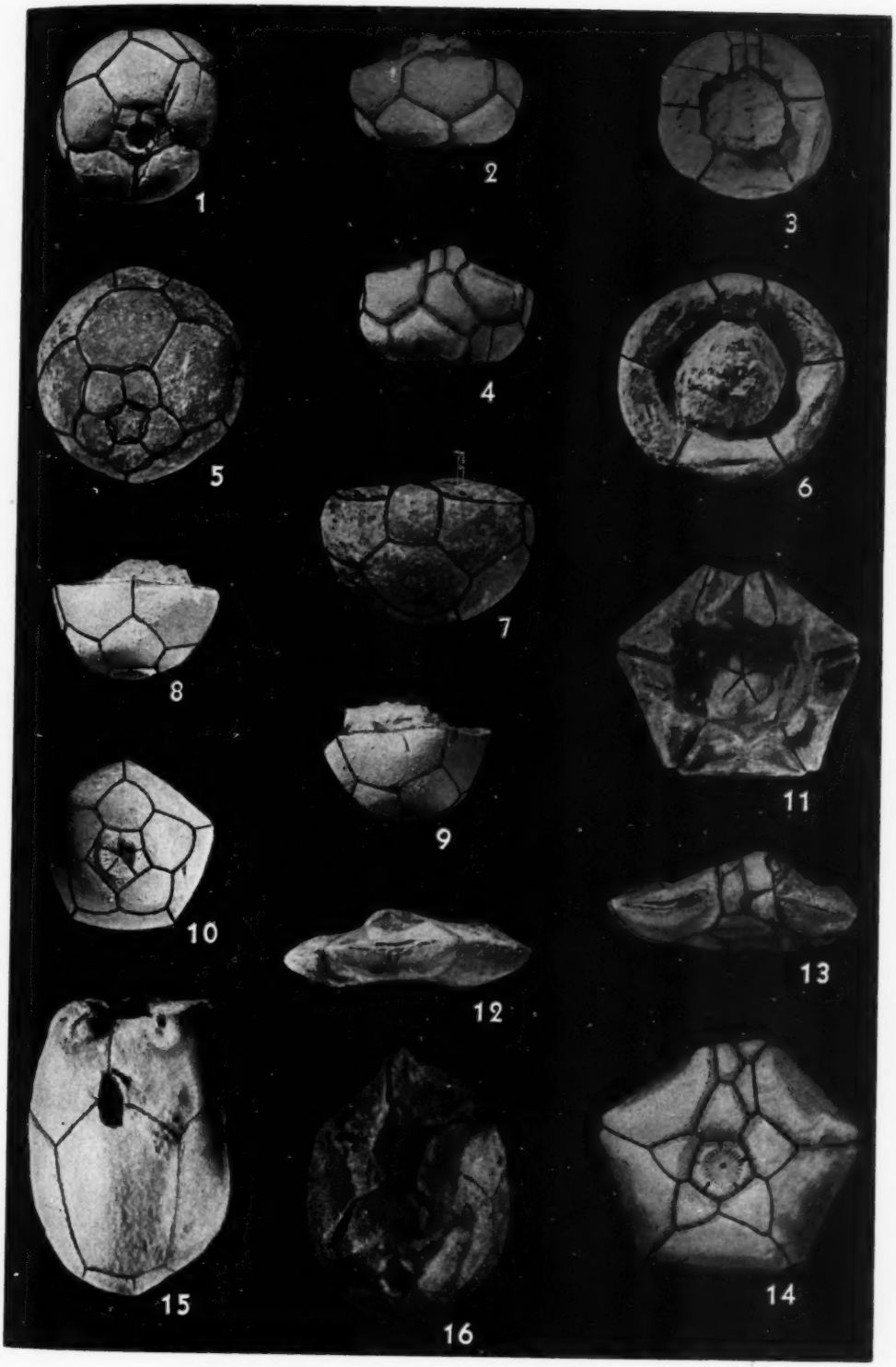
DISCUSSION

The form assigned to *Sciadiocrinus*, as *S. humilis*, n. sp., could possibly be confused with some forms of *Plaxocrinus*. However, according to the primary characteristic (basals which are not visible in side view of the dorsal cup), ascribed to *Sciadiocrinus*, the present form appears to be properly assigned to this genus.

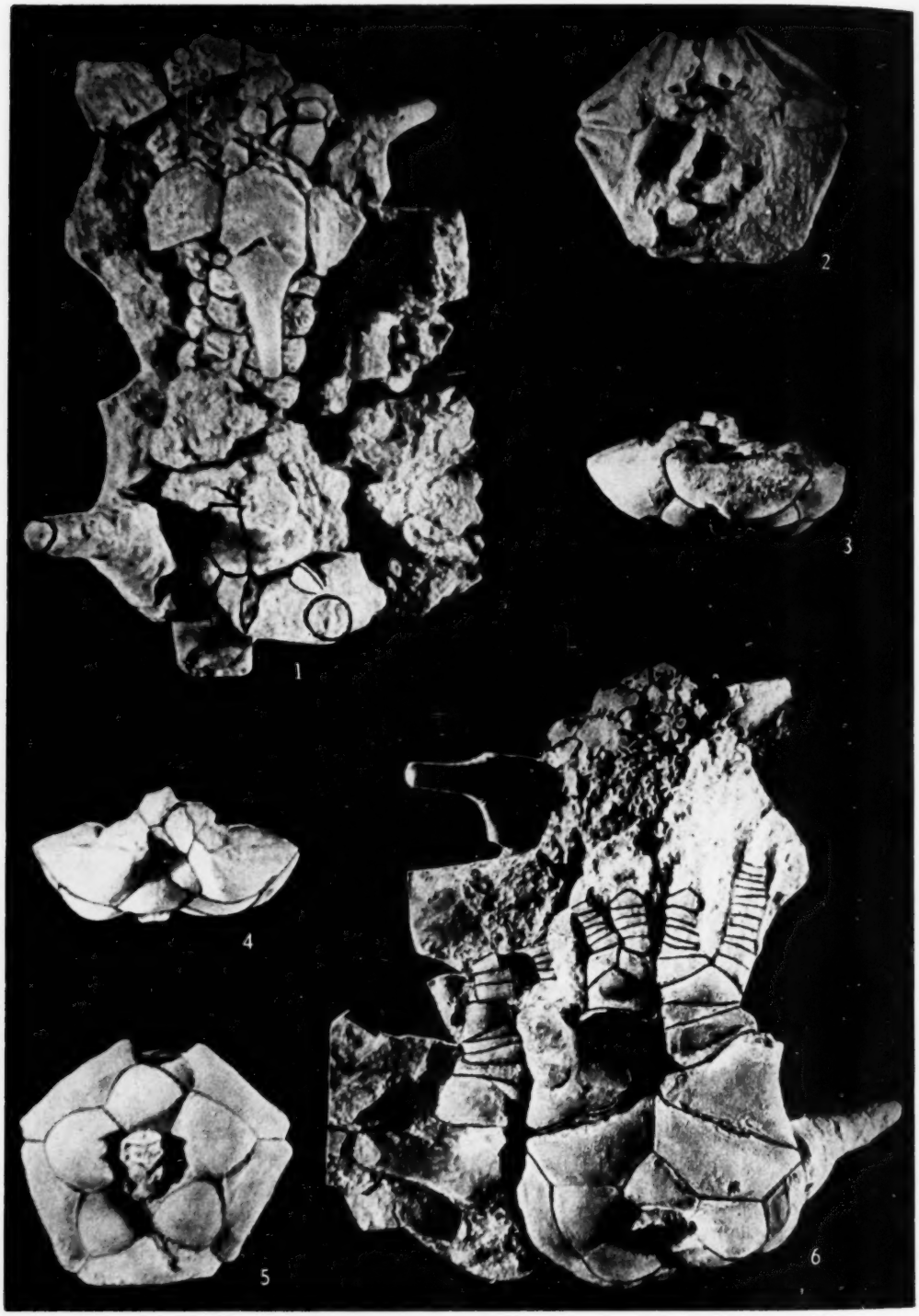
From existing evidence it appears that *Erisocrinus* first appears as a direct derivative of *Delocrinus* through elimination of the anal plate from the posterior interradius (post. IR). For forms where a decided invagination, or even mild concavity of the basal area, is present, Moore and Plummer have erected the genus *Paradelocrinus*. It is difficult to determine exactly where they consider *Erisocrinus* should take its place because some species they have referred to *Paradelocrinus* are comparable to other species they have assigned to *Erisocrinus*. The genus *Erisocrinus* is restricted by Moore and Plummer to those forms having a pentagonal outline when the dorsal cup is viewed from above or below, and the base is to have a horizontal or sub-horizontal attitude. The writer has become increasingly aware of a dominant trend toward simplicity among these late Paleozoic crinoids and is of the opinion that in the *Delocrinus-Erisocrinus* group, the shallow dorsal cup, with strongly concave base (*Delocrinus*), evolved to the relatively deep cup with sub-horizontal base (*Erisocrinus*) and on to the turbinate shaped cup with basal plane confined to the stem impression (?*Stuartwellercrinus*). The form described here as *Erisocrinus lustrum*, n. sp. provides another example of the stage between typical *Erisocrinus* and forms comparable to *Stuartwellercrinus*. The genotype species of the later genus has only three infrabasals

EXPLANATION OF PLATE 56

FIGS. *1–4*—*Dicromyocrinus periodus* Strimple, n. sp. Holotype viewed from below, anterior, above and posterior, all ×1⅔. (p. 375)
5–7—*Aesiocrinus tactilis* Strimple, n. sp. Holotype viewed from below, above and posterior, all ×1⅔. (p. 375)
8–10—*Erisocrinus lustrum* Strimple, n. sp. Holotype viewed from posterior, anterior and below, ×1¼. (p. 373)
11–14—*Sciadocrinus humilis* Strimple, n. sp. Holotype viewed from above, anterior, posterior and below, ×1½. (p. 373)
15–16—*Lecythiocrinus tubiformis* Strimple, n. sp. Holotype viewed from posterior and above, ×5. (p. 376)



Strimple, Pennsylvanian crinoids from Kansas



Strimple, Pennsylvanian crinoids from Kansas

(IBB) which may represent fusion, or perhaps it is not an actual member of the group under consideration.

The form described here as *Dicromyocrinus periodus*, n. sp. provides another representative of the Cromyocrinidae wherein three anal plates are present within the post. IR. Otherwise the specimen could, on casual examination, be referred to *Ethelocrinus compactus* (Moore and Plummer).

Plaxocrinus gloukosensis, n. sp. provides additional information as to the arm and tegmenal structure of this genus.

Assignment of the form described here as *Aesiocrinus tactilis*, n. sp., is made with considerable reluctance. The broad convex IBB circlet, which is readily visible in side view of the dorsal cup and accentuates the height of the cup, is quite different from that in normal representatives of the genus. Very probably a separate generic group will eventually be needed for the reception of such forms.

The form described as *Lecythiocrinus tubiformis*, n. sp. is smaller than most species of this genus and has very distinctive arm articulating facets.

DESCRIPTION OF SPECIES

Genus SCIADIOCRINUS Moore and Plummer
SCIADIOCRINUS HUMILIS Strimple, n. sp.
Plate 56, figures 11–14

Dorsal cup is shallow. Five IBB, five BB and the lower portions of the five RR are confined to a broad basal concavity. Post. B is slightly longer than other BB and carries a rather elongate anal X above. The narrow RA rests obliquely to the right and supports an elongate RX above. Due to the narrowness of the anal plates, the post. IR is itself rather narrow. The RR curve sharply upward out of the basal concavity to form the low outer walls of the cup. Slight notches are formed at the sutural areas between RR, which are best observed in a basal view of the cup. Outer ligamental areas are prominently impressed, and the facets slope outward.

Columnar impression is circular in outline, strongly crenulated and is pierced by a round lumen. Arms have not been observed.

Measurements of the holotype, in mm.	
Height of dorsal cup	2.7
Width of dorsal cup	23.2
Ratio of height to width	0.12
Width of IBB circlet	5.8
Height of basal concavity	1.6
Diameter of stem impression	3.9
Length of r. ant. B	4.6
Width of r. ant. B	4.5
Length of suture between BB	1.1
Length of r. ant. R	6.8
Width of r. ant. R	12.6
Length of suture between RR	4.9

Remarks.—The unusually shallow dorsal cup, with broad shallow basal concavity, distinguishes this species from other described forms.

Occurrence and horizon.—Stull shale formation, Shawnee group, Virgilian, Upper Pennsylvanian; near Melvern, Kansas.

Types.—Holotype collected by Allen Graffham. To be deposited in the U. S. National Museum.

Genus ERISOCRINUS Meek and Worthen
ERISOCRINUS LUSTRUM Strimple, n. sp.
Plate 56, figures 8–10

The dorsal cup has a low cone-shaped outline in side view, and a pentagonal outline when viewed from above or below. Five IBB expand rapidly from the stem impression and are visible in side view of the cup. Five BB are large six sided elements. Five RR are wide five sided plates and have broad horizontally directed articular facets. There are no anal plates within the cup proper, but a rudimentary element is known through a widened notch between articular facets of the radial plates.

Columnar impression is round and is pierced by a small pentagonal shaped lumen. The arms have not been observed.

EXPLANATION OF PLATE 57

FIGS. *1–6*—*Plaxocrinus gloukosensis* Strimple, n. sp. *1*, posterior view of holotype showing anal tube and umbrella-like termination; *2*, summit view of paratype; *3*, anterior view; *4*, posterior view; *5*, basal view; *6*, anterior side of holotype showing arm structure. All ×1⅞. (p. 374)

Measurements of the holotype in mm.	
Height of dorsal cup	9.2
Width of dorsal cup	17.4
Ratio of height to width	0.53
Diameter of stem impression	3.7
Length of r. ant. B	5.4
Width of r. ant. B	6.8
Length of suture between BB	3.0
Length of r. ant. R	6.1
Width of r. ant. R	6.3
Length of suture between RR	4.6

Remarks.—*Erisocrinus lustrum* is closely related to the form described as *Stuartwellercrinus argentinei* Strimple from the Wyandotte limestone formation (Missourian) of Kansas. Chief differences are in the general contour of the cup, which in *S. argentinei* is more evenly flared, and the absence of an anal notch in the articulating area in the species. The height to width ratio of *E. lustrum* is 0.53 as against 0.56 for *S. argentinei.*

At the time *S. argentinei* was presented, the author reserved placement of the species under *Stuartwellercrinus* Moore and Plummer. It is readily to be seen that *E. lustrum* represents a stage between such a typical erisocrinid as *E. typus* and the more advanced *S. argentinei.* There is nothing to be gained at this point in endeavoring to change the generic designation of *S. argentinei* and it may not prove desirable at a later date. It seems probable that *Erisocrinus* does evolve to a form closely comparable to *Stuartwellercrinus.*

Occurrence and horizon.—Near the top of Raytown limestone member, Iola limestone formation, Kansas City group, Missourian, Pennsylvanian; Lehigh cement plant quarry at Iola, Kansas.

Type.—Holotype collected by the author. To be deposited in the U. S. National Museum.

Genus PLAXOCRINUS Moore and Plummer

PLAXOCRINUS GLOUKOSENSIS
Strimple, n. sp.
Plate 57, figures 1–6

Two dorsal cups and a partially preserved crown are available for study. The crown is taken as the holotype. Five IBB are confined to the basal concavity and are almost entirely covered by the proximal columnal. Five BB are tumid plates, sweeping out of the basal concavity to become visible in side view of the cup. Five RR are tumid plates, considerably wider than long. Articulating facets do not occupy the full width of RR which is especially noticeable when viewing the cup from above or below. The facets are large and slope slightly outward. Three anal plates (anal X, RA and RX) are normally present in the post. IR, which is comparatively narrow and deep. In the holotype, RX has been pushed up out of the cup by the migratory RA.

Only fragments of the arms are preserved. First bifurcation takes place with the first PBrBr, which are protruded as stout elongate spines. A second branching appears to take place in all rays with the fourth or fifth SBrBr, which plates are tumid but not spinose. If the usual pattern is followed, the anterior rami would be asymmetrical. In the outer rays another bifurcation takes place with the fifth or sixth TBrBr, which elements are tumid but are not protruded as spines. Nonaxillary brachials are mildly wedge shaped (cuneiform) and are thin elements after the rather large SBrBr. At least 40 arms are indicated and it is thought likely the outer rays branched again before the umbrella-like tegmenal termination is reached.

The anal tube is mainly composed of circlets composed of five quadrangular shaped plates which are elaborately grooved. As the termination is approached, numerous small flattened interlocking plates appear, and the "umbrella" itself is composed of similar but larger and less ornate ossicles. Approximately nine large spine-like plates encompass the perimeter of the umbrella.

Proximal columnals have a circular outline, are rather large thin elements and are pierced by a small round lumen.

Measurements in mm.	Holotype	Figured paratype
Width of dorsal cup	29.3	26.6
Height of dorsal cup	7.1	6.0
Ratio of height to width	0.24	0.23
Height of basal concavity	2.1	1.9
Length of r. post. B	*8.8	9.0
Width of r. post. B	*9.0	7.8
Length of suture between BB	3.0	3.1
Length of r. post. R	9.0	9.1
Width of r. post. R	16.1	14.6
Length of suture between RR	6.2	5.6
Overall length of crown (approximate)	40.0	—

* Plate is slightly erratic.

Remarks.—Among described species, *P. tumulosus* Strimple from the Pumpkin Creek limestone is the most comparable form. The species are readily differentiated by the broad shallowly impressed post. IR of *P. tumulosus* as against the narrow deep post. IR of *P. gloukosensis.*

Occurrence and horizon.—Haskell limestone formation, Douglas group, Virgilian, Upper Pennsylvanian; near Homewood, Kansas.

Types.—Collected by Allen Graffham. Holotype and figured paratype to be deposited in the U. S. National Museum.

Genus DICROMYOCRINUS Jaekel
DICROMYOCRINUS PERIODUS
Strimple, n. sp.
Plate 56, figures 1–4

Dorsal cup truncate globe shaped. Five IBB form a horizontal disk which is slightly above the basal plane formed by the proximal portions of the five BB. The BB curve sharply upward from the basal area to form a good portion of the cup height. Post. B is not truncated for the reception of anal plates, but carries an elongate RA on its right shoulder. RA is unusually long, reaching the 1 post. R and carries two anal plates of approximately equal size above; the one to the left presumed to be anal X and to the right RX. Five RR form most of the outer walls of the calyx and have large articulating facets which slope just slightly outward. The area just below the outer ligamental grooves is curved inward. All cup plates are mildly tumid, with well impressed sutures.

There is no surface ornamentation of the cup plates. Columnar scar is sharply impressed, circular in outline and is rather small. Arms have not been observed.

Measurements of the holotype, in mm.	
Height of dorsal cup	9.1
Width of dorsal cup	12.8
Ratio of height to width	0.71
Width of IBB circlet	6.0
Diameter of stem impression	3.2
Length of r. ant. B	8.9
Width of r. ant. B	9.0
Length of suture between BB	4.1
Length of r. ant. R	5.1
Width of r. ant. R	9.7
Length of suture between RR	2.8
Diameter of body opening	9.2

Remarks.—*D. meadowensis* (Strimple) is the only other American species of Pennsylvanian age assigned to the genus at this writing. That species is considerably larger and the IBB have a downflared attitude. The Russian species *D. ornatus* (Trautschold) is ornamented and *D. geminatus* (Trautschold) has a more spherical shaped cup.

Occurrence and horizon.—Winterset limestone member, Iola limestone formation, Kansas City group, Missourian, Pennsylvanian; road cut along east side of hill on which the Municipal Airport is located northwest of Coffeyville, Kansas.

Type.—Holotype collected by the author. To be deposited in the U. S. National Museum.

Genus AESIOCRINUS Miller and Gurley
AESIOCRINUS TACTILIS Strimple, n. sp.
Plate 56, figures 5–7

Dorsal cup is low globe shaped. Five IBB form a broad, slightly upflared disk that is visible in side view of the dorsal cup. Five BB are large, six sided elements, that of the posterior is truncated for the reception of a rather large anal plate. Five RR are of moderate size, are pentagonal and the narrow articulating facets are typical of aesiocrinids. Anal X extends above the upper limits of the cup and is truncated for the reception of two tube plates.

Proximal columnal is sharply pentagonal shaped and is pierced by a minute pentalobate lumen. Arms have not been observed.

Measurements of the holotype, in mm.	
Height of dorsal cup	12.3
Width of dorsal cup	19.7
Ratio of height to width	0.62
Diameter of stem impression	4.0
Length of r. ant. B	10.0
Width of r. ant. B	10.0
Length of suture between BB	5.2
Length of r. ant. R	7.0
Width of r. ant. R	10.7
Length of suture between RR	3.2

Remarks.—The Mississippian genus *Cymbiocrinus*, which is a member of the Ampelocrinidae, has IBB visible in side view of the dorsal cup. There is no previously described species among the Pennsylvanian ampelocrinids having this characteristic. *A. tactilis* apparently represents a trend toward the primitive type cup which has

previously been noted as occurring among the erisocrinids.

Occurrence and horizon.—Near the top of the Raytown limestone member, Iola limestone formation, Kansas City group, Missourian, Pennsylvanian; cement quarry at Iola, Kansas.

Type.—Holotype collected by Richard Alexander. To be deposited in the U. S. National Museum.

Genus LECYTHIOCRINUS White
LECYTHIOCRINUS TUBIFORMIS
Strimple, n. sp.
Plate 56, figures 15, 16

Dorsal cup is elongate and more or less tubular shaped. Three unsymmetrical IBB expand rapidly and attain almost the entire width of the cup. The smaller IB is in right-posterior position. Five BB are elongate, six sided plates, and form more than half the height of calyx. Five RR are five sided plates which are narrower in upper portions than in the proximal region. Radial articulating facets are small protruded areas which occupy unusually small portions of the RR. The areas on each side of the facets curve inward and restrict the opening to the body cavity. Narrow ambulacral grooves extend from the articulating facets to the body cavity.

An oval shaped anal opening is present at the meeting of post. B with right and left posterior RR. The stem impression is very small and is circular in outline. The entire surface of the cup appears porous under magnification. Arms have not been observed.

Measurements of the holotype, in mm.	
Height of dorsal cup	9.7
Width of dorsal cup	6.0
Ratio of height to width	1.62
Diameter of stem impression	0.6
Length of r. ant. B	5.8
Width of r. ant. B	3.2
Length of suture between BB	3.2
Length of r. ant. R	3.5
Width of r. ant. R	3.4
Length of suture between RR	2.9

Remarks.—Two features make this species readily separable from other described species: 1) the proportionately narrow arm articulating facets, 2) the regular, almost tubular outline of the calyx.

Occurrence and horizon.—Near the top of the Raytown limestone member, Iola limestone formation, Kansas City group, Missourian, Pennsylvanian; cement quarry at Iola, Kansas.

Type.—Holotype collected by Allen Graffham. To be deposited in the U. S. National Museum.

MANUSCRIPT RECEIVED APRIL 20, 1950.

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A NEW SPECIES OF *HERCOGLOSSA* FROM MARACAIBO

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ABSTRACT—At Cañada Honda, just west of Maracaibo, a thin ferruginous sandstone bed in Sutton's Las Flores formation (upper Eocene) has yielded several nautiloids. These represent a new species of *Hercoglossa*, for which the name *H. maracaiboensis* is proposed. It is close to *H. mcglameryae* Miller and Thompson of the Midway group (Paleocene) of the North American Gulf Coastal Plain.

IN HIS well-known report on the geology of the Maracaibo basin, Sutton (1946, pl. 7, figs. 1, 2) figured two nautiloids from his upper Eocene Las Flores formation at Cañada Honda, just west of the city limits of Maracaibo, Venezuela. These are incomplete internal molds, though a replacement of portions of the test adheres to the larger individual. Both are septate throughout, and they were correctly referred to Conrad's genus *Hercoglossa*.

Sutton's work appeared while Miller's monograph of the Tertiary nautiloids of the Americas was in press. However, in an addendum to that volume, attention is called to the published illustrations of the Maracaibo specimens. Also, a non-septate fragment from the same horizon and locality is briefly treated (Miller, 1947, p. 114, pl. 100, figs. 2, 3); because of the shape of its conch, this specimen is referred with question to the genus *Aturia*, but its affinities are stated to be "very uncertain, for its sutures are entirely unknown."

Recently Mrs. Katherine V. W. Palmer of the Paleontological Research Institute kindly loaned us for study both of the specimens illustrated by Sutton, and six additional ones were collected by Dr. W. M. Furnish at the same locality. Accordingly, we now have nine from there. All are lithologically similar, and they do not seem to differ materially in size or in shape, though they are, to be sure, incomplete and more or less crushed and distorted. All in all, there seems to be every reason to believe that they represent only one species. The sutures of the septate specimens indicate clearly that the generic affinities are with *Hercoglossa*, though the conch is somewhat narrower than in typical representatives of that genus.

HERCOGLOSSA MARACAIBOENSIS
M. & C., n. sp.
Plate 58, figures 1, 2

Hercoglossa sp. SUTTON, 1946, Am. Assoc. Petroleum Geol., Bull., vol. 30, p. 1681, pl. 7, figs. 1, 2; MILLER, 1947, Geol. Soc. America, Mem. 23, p. 114.

Aturia? sp. MILLER, 1947, Geol. Soc. America, Mem. 23, p. 114, pl. 100, figs. 2, 3.

The largest and most nearly complete of the types is being designated the holotype (pl. 58, figs. 1, 2). However, the following description is based on all nine specimens.

The conch, which is thickly subdiscoidal in shape, attains a maximum diameter of more than 150 mm. and a height of at least 100 mm. The living chamber of the holotype is about half a volution in length but is not complete orad. The mature whorls are rather narrowly rounded ventrally and almost flat (very broadly rounded) laterally, and the lateral zones are considerably converged ventrad. Near the junction of the phragmacone and the living chamber of the holotype, the conch is some 65 mm. high and 55 mm. wide and the dorsal impressed zone is about 20 mm. deep. The shape of the cross section at full maturity is shown graphically by text-figure 1A. The inner volutions are relatively low and broad and are therefore more nearly typical of the genus. The umbilicus is small and inconspicuous and was probably closed by a callus. The umbilical shoulders are rounded and indefinite.

All of the type specimens are internal molds, though portions of the test (or rather a replacement of it) adhere to one of them. Furthermore, the holotype retains traces of the increments of growth, and these show that the conch bore a deep rather narrowly rounded hyponomic sinus

and on either side of it a broad rounded lateral salient. The camerae are fairly short, and in the fully mature portion of the phragmacone there are some 25 of them to the volution. At least the external sutures are rather strongly sinuous, and as shown by text-figure 2, at maturity each of them forms a high rather narrowly rounded ventral saddle and on either side of it a deep slightly asymmetrical lateral lobe, and a narrower rounded saddle which centers well outside the umbilical shoulder and which is followed by a relatively shallow broadly rounded lobe on the umbilical wall. The siphuncle is small and is located fairly close to the dorsum. Where the conch is some 40 mm. high, the siphuncle is not quite 4 mm. in diameter and its center is some 5 mm. from the dorsum.

Remarks.—The genus *Hercoglossa* was essentially world-wide in its distribution, and it ranged through the Paleocene (and possibly the Cretaceous and even the Upper Jurassic) and the Eocene, being most abundant in the Paleocene. The species under consideration is one of the youngest so far recorded, but it seems to resemble most closely *H. mcglameryae* Miller and Thompson of the Midway group (Paleocene) of Alabama. In both of these forms, the conch is narrower than is that of typical *Hercoglossa*, and in the one we are studying it is particularly so (cf. text-figs. 1A, 1B). These two species can also be differentiated by the fact that in the Midway form the sutures are somewhat more strongly sinuous (cf. text-figs. 2A, 2B), and the siphuncle is located ventrad rather than dorsad of the center of the conch. Because of the great disparity in the age of the two species, it may well be that their relationship is more apparent than real. Congeneric forms have been described from Trinidad and Peru, but they have relatively wide conchs, and

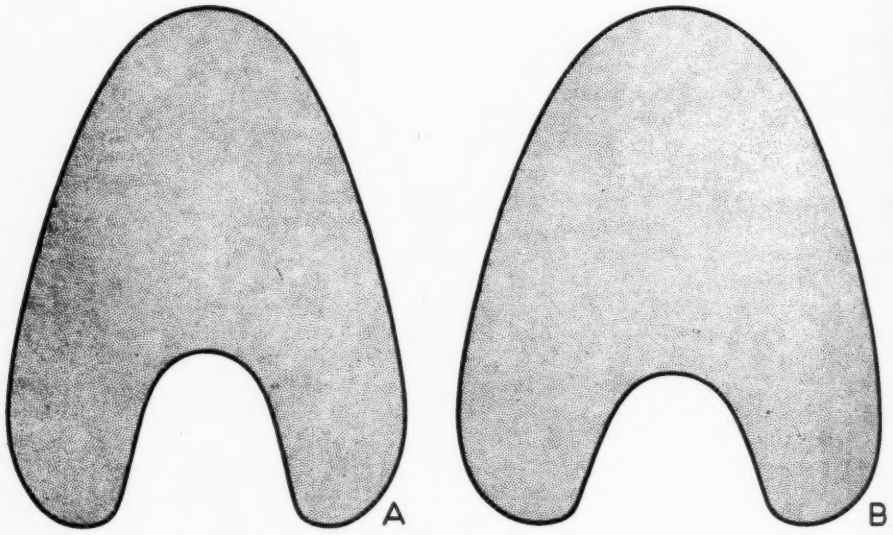

FIG. 1—Cross sections of the conchs of (A) *Hercoglossa maracaiboensis* M. & C., n. sp., ×1, and (B) *H. mcglameryae* Miller and Thompson, ×⅔. The former represents the mid-portion of the outer volution of the holotype of the Venezuelan species, the latter the adoral end of the holotype of the other species.

EXPLANATION OF PLATE 58

FIGS. 1, 2—*Hercoglossa maracaiboensis* M. & C., n. sp. Ventral and lateral views of the holotype, from a red sandstone in Sutton's Las Flores shale (upper Eocene) at Cañada Honda, near Maracaibo, Venezuela, ×⅚. (p. 377)

Miller and Collinson, *Hercoglossa* from Maracaibo

most of them are known to have come from beds that are older than those which carry *H. maracaiboensis*. Also, the genus is probably represented in the Paleocene? of Bonaire, but little information is available in regard to the Tertiary nautiloids of that island.

Occurrence.—Thin ferruginous sandstone bed in upper Eocene Las Flores formation (of Sutton) along small quebrada near government brick plant about 880 m. S. 40° E. of well Sibucara-4 at Cañada Honda, just west of city limits of Maracaibo, Venezuela (immediately west of Creole Petroleum Corporation serial no. 3439½). Associated with abundant fauna of other molluscs, echinoids, decapod crustaceans, etc.

Types.—State University of Iowa, 9541 (holotype), 9542 (paratype—text-fig. 2A), and 9543 (four unfigured paratypes); Paleontological Research Institute, 20135 (two specimens bearing the Creole serial no 3439½ and figured by Sutton in 1946—his illustrations are slightly more than ×½); and University of California (Berkeley), 31282 (specimen figured by Miller in 1947).

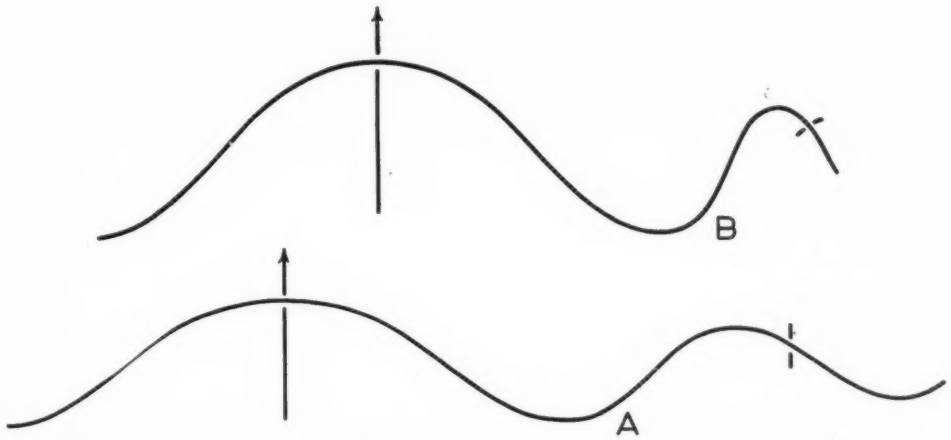

FIG. 2—Diagrammatic representations of sutures of (A) *Hercoglossa maracaiboensis* M. & C., n. sp., ×1, and (B) *H. mcglameryae* Miller and Thompson, ×¾. The former is based on a paratype (State Univ. Iowa, 9542) where the conch is some 65 mm. high, the latter on the holotype where the conch is some 75 mm. high.

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MISSISSIPPIAN CUNEATE CORALS

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ABSTRACT—Cuneate corals are compressed parallel with the cardinal-counter plane. Species are known among three families and six genera or subgenera. Arguments are advanced that larvae oriented themselves with regard to current direction and that later curvature of the corallite depended upon current action. Cuneate corals were streamlined and therefore were successfully adapted for life in marine currents. *Triplophyllites* is divided into subgenera on the basis of direction of curvature. Species-groups are erected on the nature of flattening. The following species are revised: *Cyathaxonia venusta*, *Zaphrentis ulrichi*, *Z. acuta*, *Z. elliptica*, *Z. carinata*, *Z. clinatus*, *Z. capuliformis*, *Z. reversa*, *Z. compressa*, and *Z. lanceolata*. A new variety is named.

INTRODUCTION

THE great majority of Mississippian corals were formerly referred to "*Zaphrentis*" (misapplication and misspelling of *Zaphrenthis*). Any conical coral with simple morphology was thrown into this catch-all so that eventually the generic reference became meaningless. Groups of zaphrenthids subsequently were segregated into other or new genera, but there still remain some species assigned to this primitive generic concept.

Among the most difficult of paleontologic problems is the assignment of creatures whose hard parts contain relatively few morphologic features. The simple "zaphrenthids" have been neglected because they do not have enough characters to enable them to be identified as readily as can be many other corals. Corals reviewed in this study have, for the most part, only a compressed cup containing septa, a cardinal fossula, and tabulae. Differentiation of systematic categories among these corals rests upon the closer study of a few features, rather than upon emphasis of some outstanding morphologic specialization such as colonial habit, dissepiments, carinae, tabellae, lamellae, etc. Nevertheless, the simple "zaphrenthids" discussed below are distinctive in their own way and can be used confidently in stratigraphic work.

When fossils with simple morphology are described cursorily and figured indifferently, the difficulties attendant upon their identification are increased disproportionately. Not only do these factors concern the present corals, but in addition there has been a bland disregard of prior studies on part of some systematists. Finally, the corals treated herein are variable and hence are conducive toward frustrating field applications of paleontology to stratigraphy.

METHODS OF STUDY

Having successfully avoided becoming involved with the simple "zaphrenthids" for some time, the writer was brought up against the problem again by seeing a simple compressed "zaphrenthid" from the collection of Dr. Alexander Stoyanow. A search of the literature revealed several species but their relationships were obscure and their distribution questionable. The writer therefore resolved to restudy the species concerned.

Through the financial assistance of the University of Southern California, the writer was enabled to visit several museums where pertinent material is available. All known types and comparative materials were located and studied in detail. In addition, considerable field work was done in Indiana and Kentucky to ascertain the exact occurrence of these fossils in place. Many of the type localities have been visited by the writer either as mentioned above or during previous years.

Inasmuch as these simple corals do not contain important morphologic features hidden within their inner recesses, it was not necessary to conduct extensive thin section studies. Early stages usually could be observed in immature specimens rather than by making sections.

STRATIGRAPHY

The pertinent areas of outcrop are along the Mississippi River in Iowa and Missouri and thence about 300 miles to the east across the Eastern Interior Basin in central and southern Indiana.

In Fig. 1(p. 382) the average thicknesses of the formations are given. Lithologies are those of each area of outcrop, not of any particular section. One is impressed with the increasing shaliness of the Warsaw southward in Indiana. Moreover, the Salem limestone thins into Kentucky and may be locally absent there. Subsurface studies demonstrate that Burlington-Keokuk limestones along the Mississippi River grade very abruptly into shales in western Illinois (Payne, 1940, p. 232, fig. 3); where these strata reappear as outcrops in Indiana, the calcareous facies of the Burlington-Keokuk is still missing and the silty shales are known as the Borden group.

ECOLOGY

Although the Burlington-Keokuk limestones are quite fossiliferous in the region of their type sections, the beds of the same age in Indiana and Kentucky are sparsely fossiliferous. The difference is related to the change from calcareous to shaly environment. Only where the Borden group becomes locally calcareous (as at the famous Button Mould locality near Louisville, Kentucky, or at the equally renowned crinoid bioherms at Crawfordsville and Lobo, Indiana) can one collect many fossils. For this reason, the parallel development of corals in the Indiana-Kentucky region and in the Iowa-Missouri region has not been substantiated for those species of pre-Meramecian age.

Similar ecologic conditions apply to the progressive increase in shaliness of the Warsaw and Salem limestones southward in Indiana. Corals are commonest in the calcareous facies and are rare or absent elsewhere. Some very notable examples of the preference of the rugose corals for a limy environment can be studied in alternating shale and limestone sequences in Indiana. At locality 7, for instance, the Borden-Harrodsburg contact consists of a transitional alternating series of shales and limestones. Corals are nearly confined to the limestones.

ACKNOWLEDGEMENTS

The writer is indebted to Dean A. S. Raubenheimer of the University of Southern California for arranging financial assistance to enable the writer to visit museums and carry on certain necessary field investigations. It is gratifying to acknowledge the assistance of Drs. A. L. Bowsher, G. A. Cooper, and A. R. Loeblich, Jr., of the U. S. National Museum; Mr. Guy Campbell, of Corydon, Indiana; Dr. Otto Haas, of the American Museum of Natural History; Dr. L. R. Laudon of the University of Wisconsin; Dr. E. R. Stumm, of the Museum of Paleontology at the University of Michigan; Dr. A. K. Miller, of the State University of Iowa; Drs. Gilbert Ranson and J. Alloiteau of the Museum d'Histoire Naturelle in Paris, France; Dr. H. W. Scott, of the University of Illinois; Dr. Alexander Stoyanow, of the University of Arizona; Dr. H. B. Willman, of the Illinois State Geological Survey; and R. L. Work, Librarian of the Museum of Comparative Zoology at Harvard University for lending specimens or providing pertinent information.

MORPHOLOGICAL MODIFICATIONS

Compressed corals have long been known, but only one type of compression has been discussed in any detail. Grove (1935, pp. 355–358) recognized the flattening of the cardinal or of the counter side of several species of rugose corals and named these "calceolid" corals in allusion to their having the shape of a slipper. One of these calceolid corals, *Lophophyllum calceola* White and Whitfield, in 1862, occurs in Mississippian strata. It is the type of the subgenus *Hapsiphyllites* Easton, 1944, hereinafter emended.

The corals restudied here are compressed, but the compression involves the alar sides of the corallite, that is, it is bilateral and parallel to the cardinal-counter plane. In comparison, it is arranged at right angles to that in the calceolid corals. Inasmuch as the resulting shape is that of a wedge, the English word "cuneate" is proposed (from

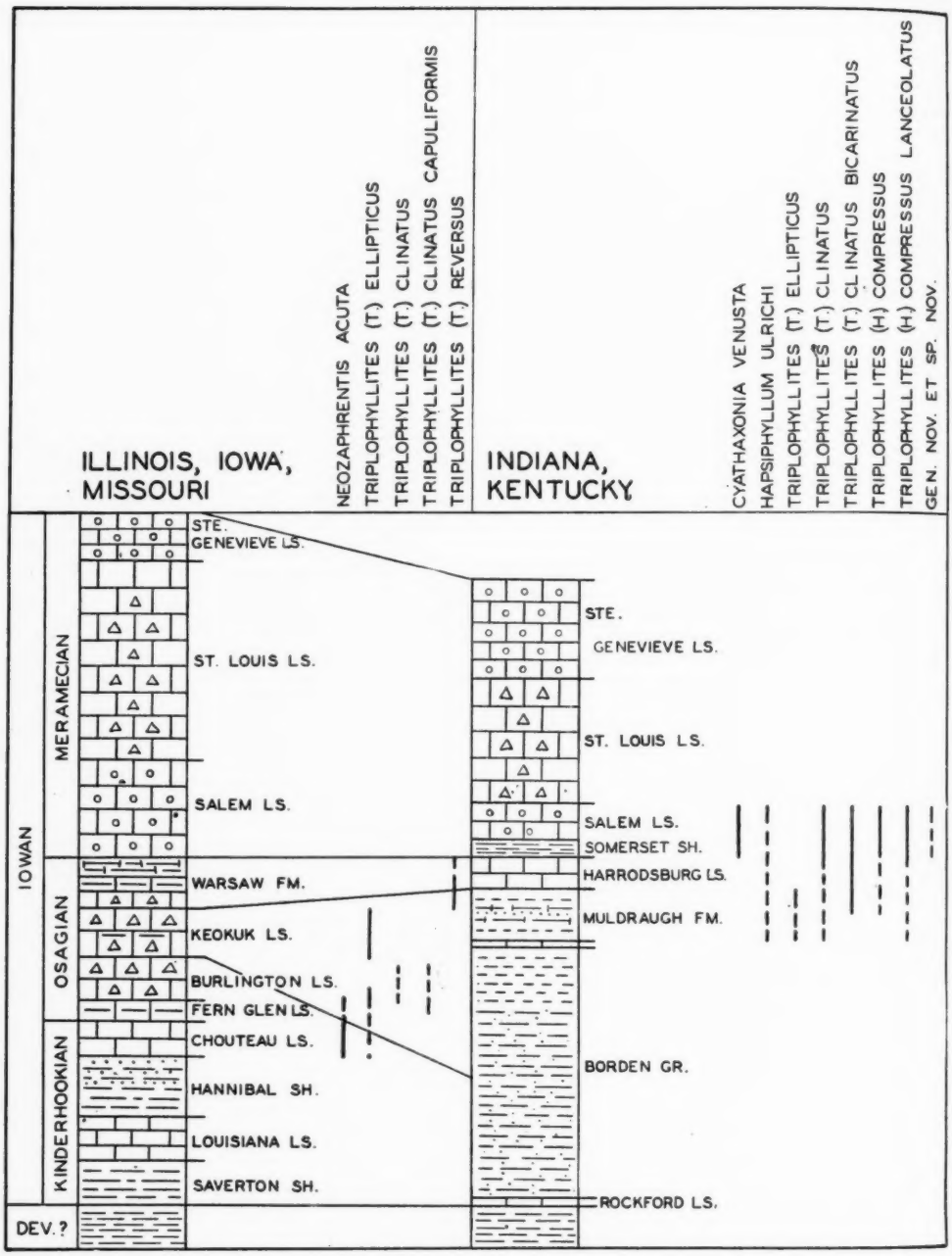


FIG. 1—Composite columnar sections of strata within the Iowan series of Illinois-Iowa-Missouri and Indiana-Kentucky. The stratigraphic range of each species is shown by vertical lines to the right of the appropriate columnar sections. Correlation lines between sections are not intended to affect the vertical ranges of species.

the Latin cuneus, wedge) as a term descriptive of this morphological modification.

As among the calceolid corals, the cuneate corals belong to several different groups: in this case being *Cyathaxonia*, *Homalophyllites*, *Hapsiphyllum*, *Neozaphrentis*, *Triplophyllites*, and an unnamed new genus. The cyathaxonid corals and the zaphrenthid corals have somewhat different modes of septal insertion and therefore are quite distantly related. Among corals with a zaphrenthid type of septal insertion *Hapsiphyllum*, *Homalophyllites*, *Neozaphrentis*, and *Triplophyllites* still are not closely related, for the first genus has contratingent minor septa and the other three have straight minor septa. It follows then that the cuneate shape is present among three coralline groups of diverse initial relationship.

EVOLUTION

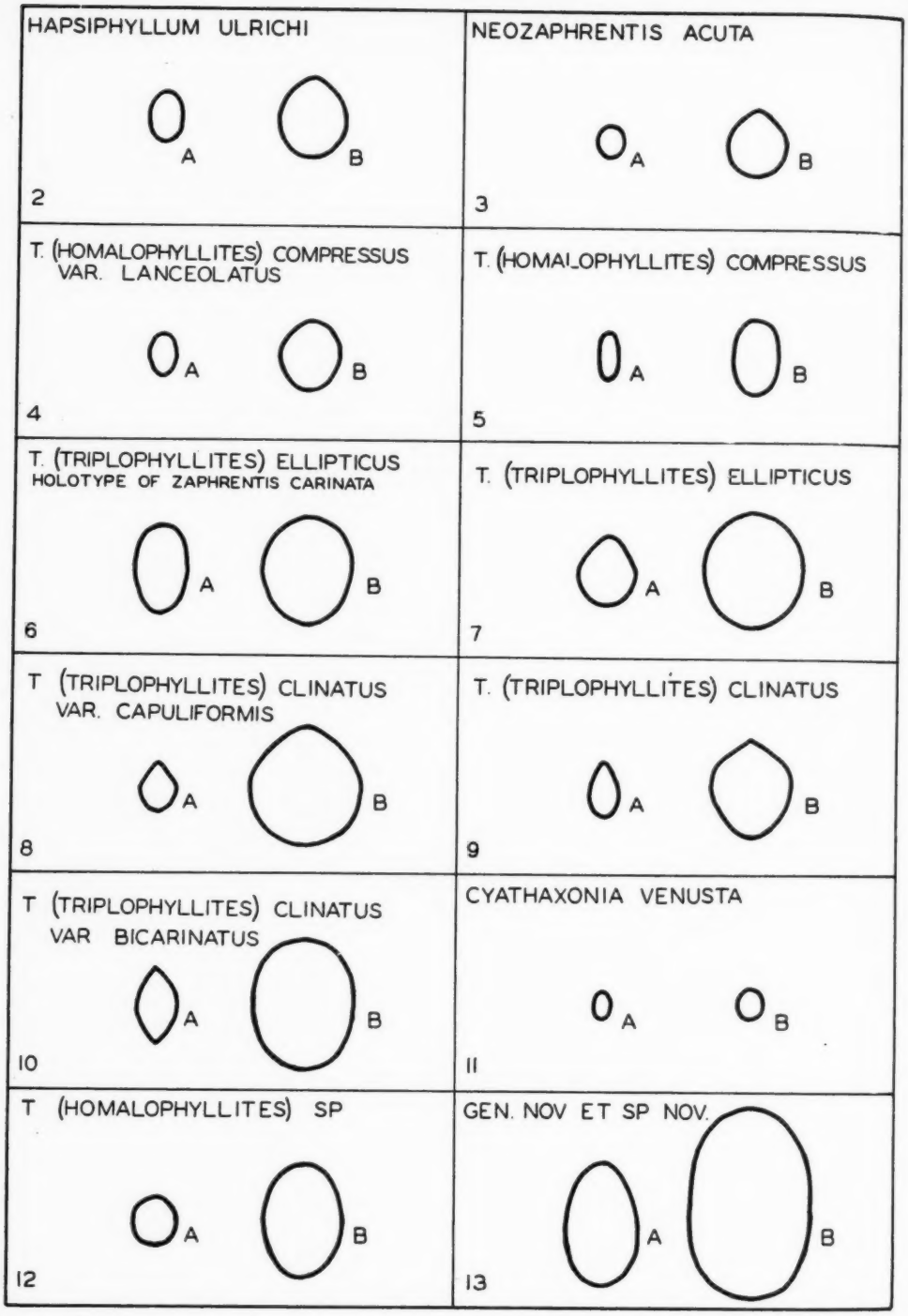
In the genera containing cuneate corals a similar developmental relationship exists. In earlier (or sometimes in contemporaneous) strata perfectly normal species belonging to a particular genus occur. That is, the zaphrenthid or cyathaxonid genera contain the features characteristic of the genotype. At some subsequent time (or as a result of apparent radiation) one or more morphologic features of less than generic rank are introduced. Some corals may become reoriented so that the cardinal fossula is on the convex side. Some corals become cuneate and either have the dominant or reoriented fossular position. Other corals become calceolid. From a stratigraphic point of view it is curious that the cuneate shape reaches its acme at about the same time in different genetic strains. From a biologic point of view it is curious that the particular strains which are cuneate or calceolid become so just before their disappearance from the geologic record.

It is quite apparent that there is only remote genetic relation between the various groups. The cuneate shape, therefore, must arise either because of orthogenetic tendency or by selective adaptation to environment. The corals discussed herein can be used to erect an argument for orthogenesis more far-reaching than that constructed on the basis of titanothere evolution, because the relationships are more diverse taxonomically among these particular anthozoans. By the same token, the arguments against such an interpretation are equally as forceful as those concerning titanothere evolution, and perhaps more so, for the corals are so simple that one can not be absolutely certain whether he is dealing with genetic strains or with parallel development. No entirely satisfactory method is known to the writer whereby a cuneate corallite will ensue from normal ancestors. No difficulty is encountered in explaining how a calceolid coral arises—as a matter of fact, two methods are known. In the first instance the calceolid coral may be equipped with an operculum which requires a straight side for hingement. In the second instance the corals may become flattened as an accommodation to bottom-dwelling habit, the corallite becoming flattened in recumbent species.

The cuneate corals are not known to have been operculate. Moreover, with two flattened sides it is hard to imagine one operculum having two hinge lines, but of course one can say that these forms had two opercula, each with its own hingement, but that they were not preserved or have never been found. In these cases nothing is gained in the way of intelligence.

Likewise, it is difficult to see how the flattening could be influenced by growth habit as in calceolids, for the corallites are flattened on two opposing sides. It hardly seems reasonable to conclude that they shifted their recumbent position from side to side.

About the only clue as to what function the keeled shape served lies in the sedimentary record of the region. During early Iowan time the seas covering the central states were moderately shallow and currents were not very strong. The limestones tend to be dense and crystalline and to occur in massive strata. By later Iowan time—specifically, at the beginning of the deposition of the Warsaw formation—the currents became stronger, presumably in accordance with a slight shallowing of the seas. Impure, thin-bedded, shaly limestones tend to be the dominant type of Warsaw sediment, but these grade laterally into granular limestones which may be oolitic. Above the



FIGS. *2–13*—Cross-sections of cuneate corals. In each pair, *a* is taken one-third of the distance from the calyx and *b* is at the calyx. All figures except *4, 12, 13* are of the holotypes, 1×.

Warsaw the succeeding limestones of the Iowan series are commonly oolitic and cross-bedded and are in large part shallow water deposits. It is in these sediments that the cuneate shape is best developed.

Two features concern explanation of the development of cuneate shape. These are the response to current-dwelling and the obtaining of food. Perhaps the elliptical shape was an adaptation to reduce resistance of the corals to the currents. At least the resistance would be less if the corals grew oriented with their long transverse dimensions in line with the currents. No instance is known in which a population of cuneate corals has been observed with the creatures erectly disposed, so there is not direct evidence as to how they might have been orientated on the sea floor.

The other feature is based upon observations made by Jones (1907, p. 529), who studied growth-forms of recent colonial corals in the Cocos-Keeling Islands. He reports that "vertical plates grow so that they offer their flat surfaces to the currents. The same thing is true of growths that are branching forms, for then the plane of greatest branching is that at right angles to the line of current." Jones assigned the cause of this orientation to the fact that the currents transported the food for the polyps and that the growth was directed so as to offer the most advantageous position for food-gathering.

The great majority of simple rugose corals are curved. Usually the curvature is consistently in one direction among the individuals of any one species. Moreover, most species are curved in the direction of the cardinal fossula (or it is said that the cardinal fossula is on the concave side). Very few corals are consistently erect in the form of right cones, although this may have been the archetypal habit. It would seem then, that there is a dominant tendency of ancient origin for corals to curve. The fact that the curvature is relatively constant within a species would indicate that when each larva established itself upon the substratum, it orientated itself in some characteristic position with regard to prevailing currents. Failure to do so would cause aberrant curvature of the corallite subsequently. Haphazard orientation, which seems to have existed in some species, would result in all manner of curvature with respect to location of the cardinal position. From these considerations the writer concludes that the orientation of the larva with respect to currents is probably governed by a genetic factor, whereas the curvature itself is probably due to an environmental factor. In this way it is possible to explain biologically how members of a coral species that consistently curve in one direction occasionally show aberrant curvature. This defection could arise if the larva failed to become properly oriented with respect to prevailing currents and then developed a curvature toward the food-transporting currents after the protothecae were secreted. If the tendency toward curvature in some particular direction were a genetic feature, then the aberrant curvature is harder to explain. One is reminded of the vexatious problems concerning the nature and importance of spiralling in dextral and sinistral gastropods. Sometimes it is of a genetic nature and is of apparent taxonomic value and other times it is probably due to embryologic accident.

In review, it is interesting to note that the curving of a coral so as to present the polyp's greatest surface to the currents would be in the same plane that the flattening of the cuneate corals occurs. Probably the cuneate shape is a late modification causing improvement in streamlining of the corallites whose orientation and tendency toward curvature are of early standing. Cuneate shape seems to be of a genetic nature within any species, for this feature is always developed in the same way, regardless of aberrations in curvature.

Currents were not peculiar to post-Iowan seas. Low velocity currents are known even in abyssal waters, so light currents obviously ran in the epeiric seas of Lower Mississippian time in the Midwest. In post-Iowan time, however, the currents seem to have increased in velocity. The culmination of the cuneate shape coincides with the presence of strong currents.

SYSTEMATIC PROBLEMS

Several species of corals which resemble each other in general appearance possess dissimilar internal morphology. Genetic

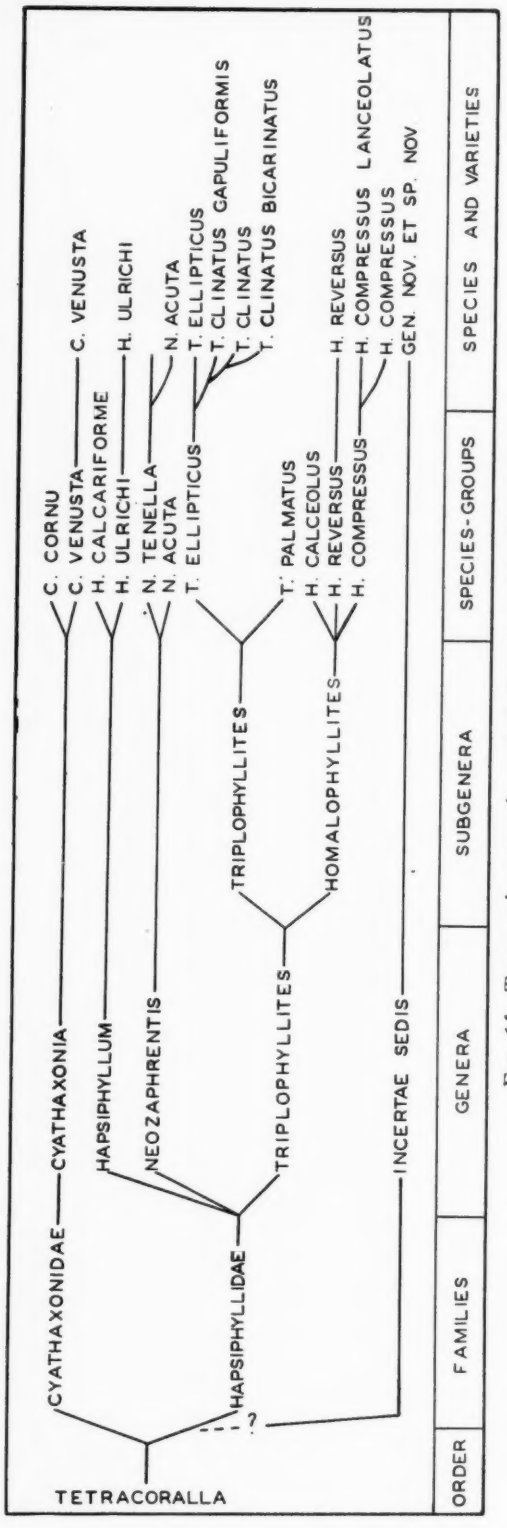


FIG. 14—Taxonomic categories and phylogeny used in this paper.

relationship is presumed to be manifest when coral species contain the same morphologic features but in different degrees of development. Accordingly, the corals considered below can be divided into four genetic groups, all of which contain thecae, septa, tabulae, and some indication of a cardinal fossula, but which individually may be characterized as follows:

Cyathaxonia.—Has "cyathaxonid" order of septal insertion and a columella.

Triplophyllites.—Has "zaphrenthid" order of septal insertion and usually has dissepiments at some stage in development. Usually is conical, rather than being cylindrical or flaring.

Neozaphrentis.—Has "zaphrenthid" order of septal insertion and cardinal fossula bounded by unfused inner edges of septa.

Hapsiphyllum.—Has "zaphrenthid" order of septal insertion, contratingent minor septa and lacks dissepiments.

The only reason that it becomes necessary to consider these genera together is that the shapes of the individuals of some species are unique and the same in each group. The species of different or even similar genera would possibly be considered to be conspecific if only external features were observed. Likewise, different species within a genus may resemble each other in their curious shape, yet be otherwise specifically separable. The first of these conditions (similar but unrelated species) is commonly termed isomorphism. The latter condition (similar related species) is commonly called homoeomorphism. Inasmuch as both conditions are found among cuneate and calceolid corals, the first problem to be settled involves distinguishing between isomorphs and homoeomorphs. Otherwise, any proposed classification would be deficient.

Simple corals are most commonly in the shape of a curved cone with a circular cross-section throughout. Cuneate or calceolid corals usually tend toward a "normal" cross-section at some stage in their ontogeny and hence are considered to be modifications of the original round stock. Among the simply organized creatures considered herein, the cuneate or calceolid modification is the principal feature by means of which isomorphism or homoeomorphism is manifested. Therefore, these modifications of existing structure are given a subordinate

position in the systematic arrangement of the species. Major modifications are considered to be of specific value, whereas minor modifications of these in turn are considered to be of varietal magnitude.

The second problem concerns the systematic importance to be attached to curvature of the coral. Four orientations are known: (*a*) the cardinal fossula is on the concave side when the corallite is viewed from either alar side; (*b*) the cardinal fossula is on the convex side with similar orientation; (*c*) the cardinal fossula is variably located; (*d*) the corallite is a right cone, that is, it is not curved, and hence, the cardinal fossula is not demonstrably on one side or another.

Case *d* is rarely encountered. Case *c* is known but is not common. It is, however, common among groups of specimens of *Zaphrentis calcariformis* Hall, 1882. In a large number of specimens one finds that more than half of them have the cardinal fossula on the concave side. Among the other specimens, some will be contorted so that the position of the fossula varies in one specimen. Some will be contorted or straight and the fossula will be in some position of greatest concavity. Others will, more rarely, have the fossula somewhere on the convex half of the coral. Lastly, some specimens may have elongate scars of attachment in the apical portions of the corallites and then may be curved or contorted distally; in both these latter instances, the trace of the cardinal septum usually lies along the greatest diameter of the scar of attachment. In the majority of all foregoing conditions, the cardinal fossula is somewhere on the concave side, even though it may not be at the place of greatest concavity.

Even though some variation in the location of the cardinal fossula with respect to curvature is established, the writer still considers the character to be of taxonomic value. After all, its variable location is merely a manifestation of the natural tendency of organisms to vary. It would seem, then, that *Z. calcariformis* Hall is merely a species from which one could expect a new strain of corals to evolve, with the cardinal fossula located on other than the concave side. Viewed in this fashion, the species becomes additionally significant from an evolutionary standpoint.

It is a well-known fact that the counter quadrants of rugose corals usually contain more major septa than do the cardinal quadrants. Inasmuch as the rugose corals are commonly curved toward the cardinal septum, it naturally follows that the counter quadrants are potentially expanded (as if they were stretched around the calyx rim) by the greater curvature on that side. Additional septa occur in the counter quadrants in the expanded regions, but it is not known whether the expansion necessitates their insertion or vice versa. On the other hand, it can be observed among the corals studied herein that the counter quadrants are consistently accelerated no matter on which side the cardinal fossula lies. This runs counter to the principle observed among rugose corals in general (which mostly have their cardinal fossulae on the concave side). If the coral is convex on the cardinal side, one would assume before observing the septa that they would not be accelerated on the counter side, or even that they might be accelerated on the cardinal side. It is concluded, then, that as a general rule, the distribution of septa within the quadrants of a calyx results from a strong genetic requirement. Moreover, deviations from the normal situation are usually minor in effect. If these conclusions are valid, then one may further conclude that the distribution of septa within a calyx has been determined by long established genetic lines. In other words, the distribution of septa will tend to remain constant for a time even though the shape of the coral may begin to change. From these matters, the writer has concluded that the orientation of the cardinal fossula with regard to curvature is less important taxonomically than is the nature and degree of acceleration of the septa. Accordingly, the location of the cardinal fossula is assigned subgeneric status.

The third problem is to arrange the various corals into such taxonomic groups that their inter-relationship is apparent, yet assuring that the cuneate (or round, or calceolid) corals of one genus or subgenus may be distinguished by a collective term from the cuneate (or round, or calceolid) corals of another higher category. The term "circulus" has been proposed (Gregory, 1896, p. 22) as a systematic group, the members of which bear the same relation to some standard species as did the rings

of listeners to each of several speakers in a Roman forum. This original usage implies lack of genetic relationship and also a rather haphazard but necessary collection. It is essentially a term to include isomorphic species. It could be used to designate all cuneate, all calceolid, or all conical corals. Circulus has been used in other senses, however, and would possibly be suitable under one of these latter, but not under its original meaning.

Vaughan (1905, p. 183) proposed "gens" for "the aggregate of all the species which possess, in common, a large number of essential properties, and are continuously related either in space or time."

It is not possible to say that the corals under discussion contain a large number of properties in common for their structure is quite simple. Yet their structure is ample enough for careful differentiation. Possibly distinctive groups of these corals could be alluded to as gentes.

On the other hand, the straight-forward appellation "species group" conveys just what is desired. Groups of species which differ collectively from other similar groups, yet whose similarities are not of generic or subgeneric rank, may conveniently be encompassed in species-groups.

SYSTEMATICS

Investigation of the following corals has revealed morphologic features not hitherto known. Philosophical consideration of relationships results in rearrangement of some genera and species previously studied by the writer. Whenever systematic reorganization is required, the writer puts forth the background and reasons for these changes.

In the following section, AMNH refers to the American Museum of Natural History. IGS refers to Illinois State Geological Survey. UA, to the University of Arizona. USC, to the University of Southern California. UI, to the University of Illinois. UM, to the University of Michigan. USNM, to the U. S. National Museum.

Phylum COELENTERATA
Class ANTHOZOA
Order TETRACORALLA
Family CYATHAXONIDAE Milne-Edwards & Haime, 1850
Genus CYATHAXONIA Michelin, 1847

Cyathaxonia cornu species-group

Diagnosis.—*Cyathaxonia* with the cardinal fossula on the concave side of the corallite and with a conical shape.

Remarks.—Most species of *Cyathaxonia* belong here.

Cyathaxonia venusta species-group

Diagnosis.—*Cyathaxonia* with the cardinal fossula on the convex side of the corallite and with a cuneate shape.

CYATHAXONIA VENUSTA Greene, 1904
Plate 61, figures 10–14; text-figure 11

1879. not *Cyathaxonia compressa* THOMPSON, Proc. Phil. Soc. Glasgow, vol. 11, no. 18, p. 197, pl. 1, fig. 6.
1899. *Cyathaxonia compressa* GREENE, Contributions to Indiana Palaeontology, pt. 2, p. 9, pl. 4, figs. 14–17.
1904. *Cyathaxonia venusta* GREENE, Contributions to Indiana Paleontology, pt. 19, p. 187, pl. 56, figs. 10–14.
1906. *Cyathaxonia venusta*. BEEDE in Beede and Cumings, Indiana Dept. Geol. Nat. Res., 30th Ann. Rept., p. 1202, pl. 11, figs. 2, 2a.
1906. *Cyathaxonia venustum*. BEEDE in Beede and Cumings, Indiana Dept. Geol. Nat. Res., 30th Ann. Rept., p. 1373.
1922. *Cyathaxonia venustum*. CUMINGS, Handbook of Indiana Geology: Indiana Dept. Cons., Pub. 21, pt. 4, p. 505.

Description of Holotype.—Corallite an elliptical cone slightly curved away from the cardinal fossula. Cross-section lanceolate near the apex and ovate near the calyx. Surface smooth except for faint traces of septa due to weathering. Theca rather thick.

Calyx shallow, 2.5 mm. deep. Septa in two orders, totaling 32. Cardinal fossula nearly parallel-sided, deep, slightly wider than other loculi. Cardinal septum extends one-third length of fossula in calyx. Counter septum similar to the other major septa but joined near its axial end by the minor septum on either side. On each side of the calyx are seven major septa which join the columella. They are a little thicker near the theca than along most of their length.

Alternating with these is an equal number of minor septa which do not extend as far distally as the majors and which lean in the counter direction to fuse with the majors just before reaching the columella. The minors are very thin most of their length but are as thick as majors near the theca. At the calyx rim major and minor septa are the same length. Columella smooth, slightly oval near the calyx floor, about 2.0 mm. high.

Dimensions.—Height 15 mm. Greatest diameter of calyx 5 mm. Least diameter of calyx 4 mm.

Description of Paratypes and Hypotypes.—The paratypes all have 32 septa also and are arranged as in the holotype. In one of the paratypes the cardinal septum is perfectly preserved and its upper edge can be seen to slope steeply into the fossula and then swing over to the columella. There is some small variation in the length of the counter septum. In some calices it is slightly longer and in others, slightly shorter than are the neighboring majors.

Greene's hypotypes are like the holotype except that they are a little more narrowly elliptical and two of them have 34 septa.

Material.—Specimens studied: nine. Holotype: AMNH Nos. 23413–23415. Greene's hypotypes: AMNH Nos. 24045–24049.

Type locality.—Greene gave the type locality as "Warsaw division of the St. Louis group" at Georgetown and Lanesville, Indiana. In terms of recent geological usage, this probably means that the fossils came from the Salem limestone (Meramecian series of the Mississippian). One particular locality in the Salem limestone at Lanesville was and is a favorite collecting locality of many paleontologists. Inasmuch as Greene had all the syntypes together (and they are similarly preserved) one might assume that they came from one locality. The only places where this species has been collected by others than Greene is from the Salem limestone at Lanesville, Paynter's Hill, and Spergen Hill, so there is some reason to believe that Lanesville is the type locality.

Localities.—12, 13 (type locality).

Remarks.—The types are all reddish silicified replacements. The writer removed red clay from the loculi between septa when studying them. At Lanesville the Salem fauna is obtained by washing red residual clay to obtain the silicified fossils.

Family HAPSIPHYLLIDAE Grabau, 1928, emend. Easton, 1944

Genus HAPSIPHYLLUM Simpson, 1900

Diagnosis.—Simple tetracorals with long contratingent minor septa. Cardinal fossula long and slender. Alar pseudofossulae more or less distinct. Counter septum joined by adjacent minors to form a tripartite structure. Tabulae present. Dissepiments absent. Cardinal fossula usually on concave side of corallite.

Genotype.—*Zaphrentis calcariformis* Hall, 1882.

Remarks.—The writer (1944, p. 42) emended the genus *Hapsiphyllum* so as to include the subgenus *Homalophyllites* Easton, 1944. This procedure brought together corals with normal short minor septa and corals with longer contratingent minor septa. Since 1944 the writer has had occasion to study in new species many more specimens of corals with contratingent minor septa. It has been concluded that this feature is stable enough to warrant separation of the subgenera *Hapsiphyllum* and *Homalophyllites*. Therefore, the emendation proposed in 1944 is considered inapplicable. The effect of this action is to suppress *Hapsiphyllum* as a subgenus and to reassign the subgenus *Homalophyllites* to another genus. (For further remarks, see under *Triplophyllites*).

Hapsiphyllum contains two parallel series of corals, one with a normal conical shape, the other with a cuneate shape. These are the basis for recognizing two species-groups in the genus.

Hapsiphyllum calcariforme species-group

Diagnosis.—*Hapsiphyllum* with a conical shape.

Remarks.—Included here are *Hapsiphyllum calcariforme* (Hall), 1882 and *Hapsiphyllum cassedayi* (Milne-Edwards), 1860.

Hapsiphyllum ulrichi species-group

Diagnosis.—*Hapsiphyllum* with a cuneate shape.

HAPSIPHYLLUM ULRICHI (Worthen), 1890
Plate 60, figures 11a–c; text-figure 2

1889. *Zaphrentis ulrichi* MILLER, N. Amer. Geol. and Paleontology, p. 210 (nomen nudum).
1890. *Zaphrentis ulrichi* WORTHEN, Geol. Survey Illinois, vol. 8, p. 76, pl. 10, figs. 10, 10a.
1898. *Zaphrentis ulrichi* WELLER, U. S. Geol. Survey Bull. 153, p. 649.

Description of holotype.—Corallite an elliptical cone, curved in the direction of the cardinal position. Cross-section somewhat more narrowly elliptical near the apex than near the calyx. Depth of calyx not known. Cardinal fossula very deep, extending slightly past the center of the calyx, and broadest in its inner portion. Cardinal septum very short near the calyx but crossing the fossula farther down. Other septa of two types: the majors fuse at their inner ends to form the fossular wall; the minors lean toward the counter position and each fuses with the next adjacent major septum about one-third of the distance to the axis. The counter septum is fused with the next adjacent minor septum on either side about half of the distance to the axis. The right cardinal quadrant contains six pairs of septa; the right counter quadrant contains seven pairs; the left counter quadrant contains eight pairs; and the left cardinal quadrant contains five pairs. Thus, the calyx contains 28 major septa (counting the cardinal septum). Alar pseudofossulae are distinct because they extend farther axially than do the neighboring loculi.

Dimensions.—Holotype, height 20 mm. Greatest diameter of calyx 11.5 mm. Least diameter of calyx 10 mm.

Material.—Specimens studied: six. Holotype and paratype, IGS (Worthen Collection) No. 2573. Topotypes, USNM No. 42743.

Type locality.—Warsaw formation (Meramecian group, Mississippian system), Colesburg, Kentucky. (Coalsburg [sic] on label).

Remarks.—The Worthen collection contains four specimens bearing the number 2573. One of these specimens, which is of different preservation than the other three, is a species of *Triplophyllites*. It is so different from the other three that it is doubtful that Worthen included it among the original types. Possibly this specimen became associated with the type labels accidentally and was so numbered.

Of the other three specimens, one, which is the basis of Worthen's figures of the species (Worthen, 1890, pl. 10, figs. 10, 10a) is hereby designated the holotype. The dimensions of the figure agree with those of the "medium size individual" mentioned in Worthen's description. The actual measurements of the specimen differ slightly from the stated measurements. One concludes that Worthen's measurements were taken from the drawings, with which they agree.

The two remaining specimens are not at all well preserved. The smallest is not identifiable. The largest specimen probably belongs to *Hapsiphyllum ulrichi*, but it is not possible to decide even how many major septa it had. Even so, it becomes a paratype. Its calical diameters are 13 mm. by 14 mm.

The largest specimen seen (USNM lot 42743) measured 34 mm. in length, with calical diameters of 15 mm. by 13.5 mm. The usual number of septa is 26, but specimens with 28 and 29 have been studied.

Occurrence.—Localities 1 (type locality), 2.

Genus NEOZAPHRENTIS Grove, 1936

Remarks.—Since Grove erected *Neozaphrentis* upon *Zaphrentis tenella*, the species *Z. acuta*, *Z. palmeri*, and *Z. parasitica* have also been referred to the genus. Of these, *Z. acuta* shows a cuneate tendency, and so it is necessary to make two species groups in the interests of consistency.

Neozaphrentis tenella species-group

Diagnosis.—*Neozaphrentis* with a circular cross section.

Neozaphrentis acuta species-group

Diagnosis.—*Neozaphrentis* with a cuneate shape.

Remarks.—*Neozaphrentis acuta* is not consistently cuneate, but it still is reasonable to establish this species group. It is probable that *N. acuta* is very close to the point of separation of the two species-groups and that the cuneate tendency is not well established in the species because only a small evolutionary period elapsed since the tendency originated.

NEOZAPHRENTIS ACUTA (White & Whitfield) 1862

Plate 61, figures 6, 7; text-figure 3

1862. *Zaphrentis acutus* WHITE & WHITFIELD, Proc. Boston Soc. Nat. Hist., vol. 8, p. 306.
1865. not *Zaphrentis acutus*? WINCHELL, Acad. Nat. Sci. Philadelphia Proc., p. 111.
1883. *Z. [aphrentis] acuta*. WHITE, U. S. Geol. Geog. Survey Terr., 12th Ann. Rept. (1878), p. 159. (Advance printing, 1880).
1889. *Zaphrentis acuta*. MILLER, N. Amer. Geol. and Paleontology, p. 208.
1894. not *Zaphrentis acuta*. KEYES, Missouri Geol. Survey, vol. 4, p. 109, pl. 13, fig. 4.
1897. not *Zaphrentis acuta*. KEYES & ROWLEY, Iowa Acad. Sci., vol. 4, p. 30.
1898. *Zaphrentis acuta*. WELLER, U. S. Geol. Survey Bull. 153, p. 644.
1908. not *Zaphrentis acuta?* ROWLEY, Missouri Bur. Mines, ser. 2, vol. 8, pp. 31, 62, 63; pl. 16, figs. 19, 20.
1908. not *Zaphrentis acute* [sic]? ROWLEY, Missouri Bur. Mines, ser. 2, vol. 8, p. 33.
1908. not *Zaphrentic* [sic] *acuta*. ROWLEY, Missouri Bur. Mines, ser. 2, vol. 8, p. 62.
1943. *Neozaphrentis? acuta*. WILLIAMS, U. S. Geol. Survey Prof. Paper 203, p. 56 (not pl. 6, figs. 31–33).

Description.—Simple corallites in the form of curved cones, rarely cuneate. Epitheca smooth, with encircling swellings. Calyx oblique, sloping down toward the concave side. Cardinal fossula very deep, axially widened, and bordered by axial ends of major septa which are only slightly fused. Holotype with 24 major septa, of which five are in each cardinal quadrant and six in each counter quadrant; cardinal septum very short; counter septum slightly longer than neighboring majors. Minor septa short. Alar pseudofossulae slightly wider than other loculi. The figured paratype has 32 major septa, with six in each cardinal quadrant and nine in each counter quadrant; cardinal septum extends across axially swollen cardinal fossula and bends to the right; counter septum longer, higher, and thicker than neighboring majors. Alar pseudofossulae distinct. Minor septa almost absent and very short. Unfigured paratype with 31 major septa, of which each cardinal quadrant contains six, the right counter quadrant contains nine, and the left counter quadrant contains eight; cardinal septum short but extends straight across the nearly vertically-walled cardinal fossula near the bottom. Counter septum longer than neighboring majors and of the same thickness. Alar pseudofussulae quite distinct. Minor septa rather short at calyx margin. Calyx very deep, about 9 mm.

Dimensions—Holotype: length about 20 mm.; calical diameters 9 mm. by 10 mm. Dimensions of figured paratype: length about 16 mm.; calical diameters 10 mm. by 11.5 mm. Dimensions of unfigured paratype: length, about 22 mm. (incomplete); calical diameters 11 mm. by 12.5 mm.

Material.—Specimens studied: three. Holotype and paratypes, AMNH No. 6366/1.

Locality.—22 (type locality).

Occurrence.—Kinderhook beds, Burlington, Iowa.

Remarks.—The holotype has a carinate counter edge, giving it a cuneate shape, but the paratypes have circular cross-sections.

This species has been imperfectly understood for many years, indeed, the accompanying figures are the first to be published of the types.

The epitheca is smooth and apparently always was, contrary to the doubtful statement in the original description that the smoothness may be due to weathering. The "transverse septa" mentioned by White and Whitfield were questionably considered to be dissepiments by Williams (1943, p. 56). It is the confident belief of this writer that the "transverse septa" are really the tabulae as understood in recent usage. Inasmuch as early American students modeled their descriptions on European works, it is reasonable to assume that the concepts of vertical and horizontal septa reflect merely the translated French equivalents from such works as Haime's. Perforations in the peripheral portions of the "transverse septa" mentioned by White and Whitfield (and visible in the types) are nothing but occasional holes mechanically broken through the tabulae.

The specimens usually called *Z. acuta* will be considered by the writer in a forthcoming paper.

Genus TRIPLOPHYLLITES Easton, 1944

Diagnosis.—Simple, medium to large, curved corals. Cardinal fossula prominent. Alar pseudofossulae usually prominent. Major septa long, minor septa short. Tabu-

lae usually well developed. Dissepiments usually sparse, commonly restricted to lower portions of the corallite.

Remarks.—When originally proposed it was stated (Easton, 1944, p. 39) that the genus might sometime be divided into two subgenera on the basis of the position of the cardinal fossula. At that time only *Zaphrentis reversa* Worthen, 1890 was thought possibly to possess the cardinal fossula on the convex side. Since that time several corals have been studied which require the division of *Triplophyllites* into two subgenera.

Subgenus TRIPLOPHYLLITES Easton, new usage

Diagnosis.—*Triplophyllites* with the cardinal fossula on the concave side of the corallite.

Type.—*Triplophyllites palmatus* Easton, 1944.

Remarks.—Most species of *Triplophyllites* belong here. It has been pointed out (Easton, 1944, p. 37) that *Zaphrentoides* may be a senior synonym of *Triplophyllites* but that the status of *Zaphrentoides* is so confused as to be (in the opinion of the writer) inapplicable at present. If the genus *Zaphrentoides* should be proved (by some future study of the genotype) to be the same as the genus *Triplophyllites*, then the subgenus *Triplophyllites* would be reassigned to the genus *Zaphrentoides*. (See under *Homalophyllites*).

The genus *Zaphrentoides* has been formally introduced into the literature of the North American Carboniferous by Moore and Jeffords for a Lower Pennsylvanian coral. These authors (Moore and Jeffords, 1945, pp. 129–130) reviewed the status of the genus and its position relative to several other genera and reached different working assumptions than the writer did in 1944. Subsequently, *Zaphrentoides* was used for certain Mississippian corals by Laudon et al. (1949, pp. 1502–1552), but without explanation. Dr. Laudon, (correspondence, 10 October 1949) informs me that the usage corresponds to what has been formerly known as *Triplophyllum*.

As interpreted herein, the subgenus contains both cuneate and normally conical corals. Two species-groups are set up to accommodate these different forms.

Triplophyllites palmatus species-group

Diagnosis.—*Triplophyllites* (*Triplophyllites*) with a circular cross-section.

Remarks.—Most species of *Triplophyllites* belong here.

Triplophyllites ellipticus species-group

Diagnosis.—*Triplophyllites* (*Triplophyllites*) with a cuneate cross-section.

Remarks.—*Zaphrentis ellipticus*, *Z. carinatus*, *Z. capuliformis*, *Z. clinatus*, and a new variety of the last species are referred to this species-group.

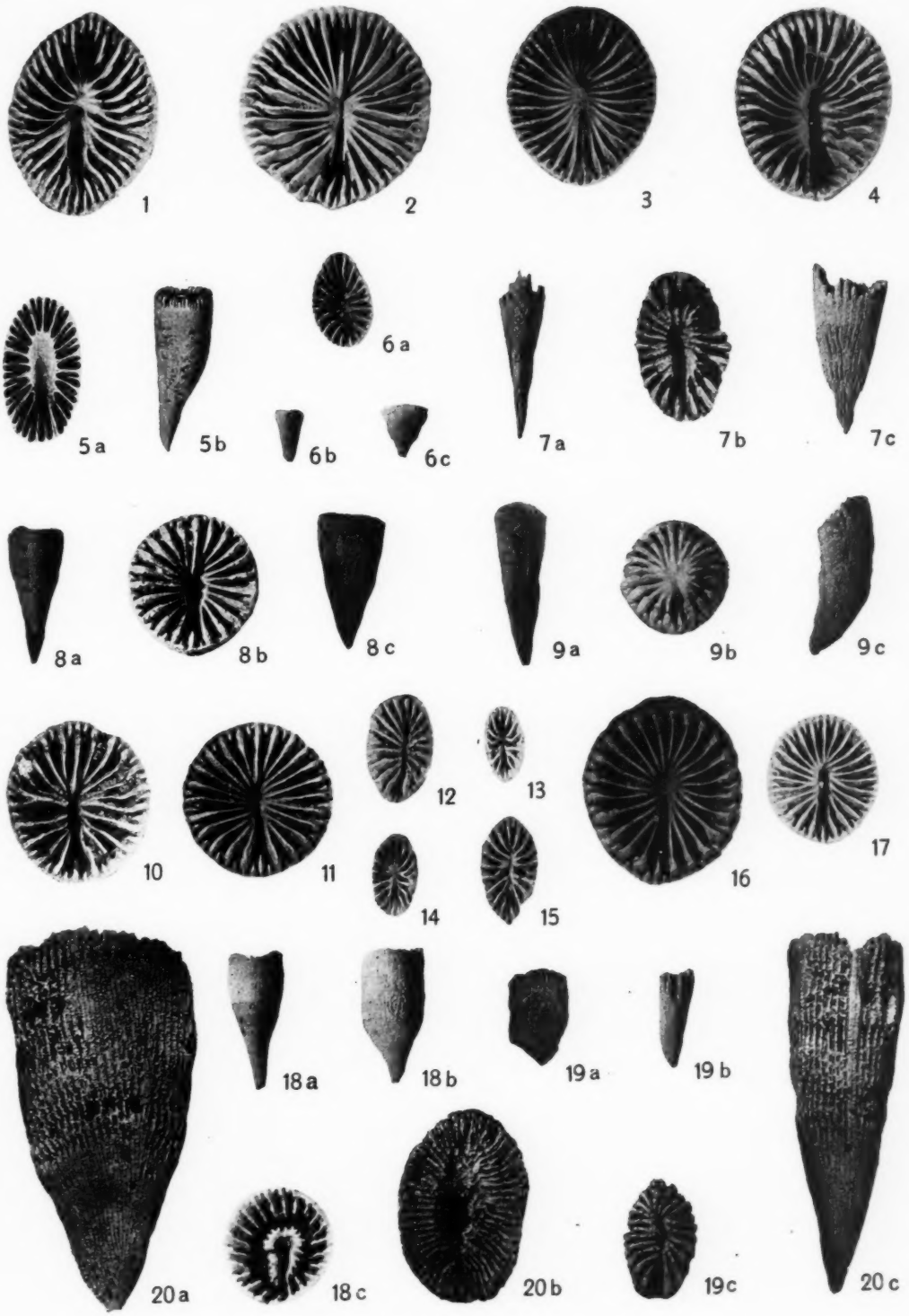
EXPLANATION OF PLATE 59

Calyces 2× except as otherwise indicated; lateral views 1×.

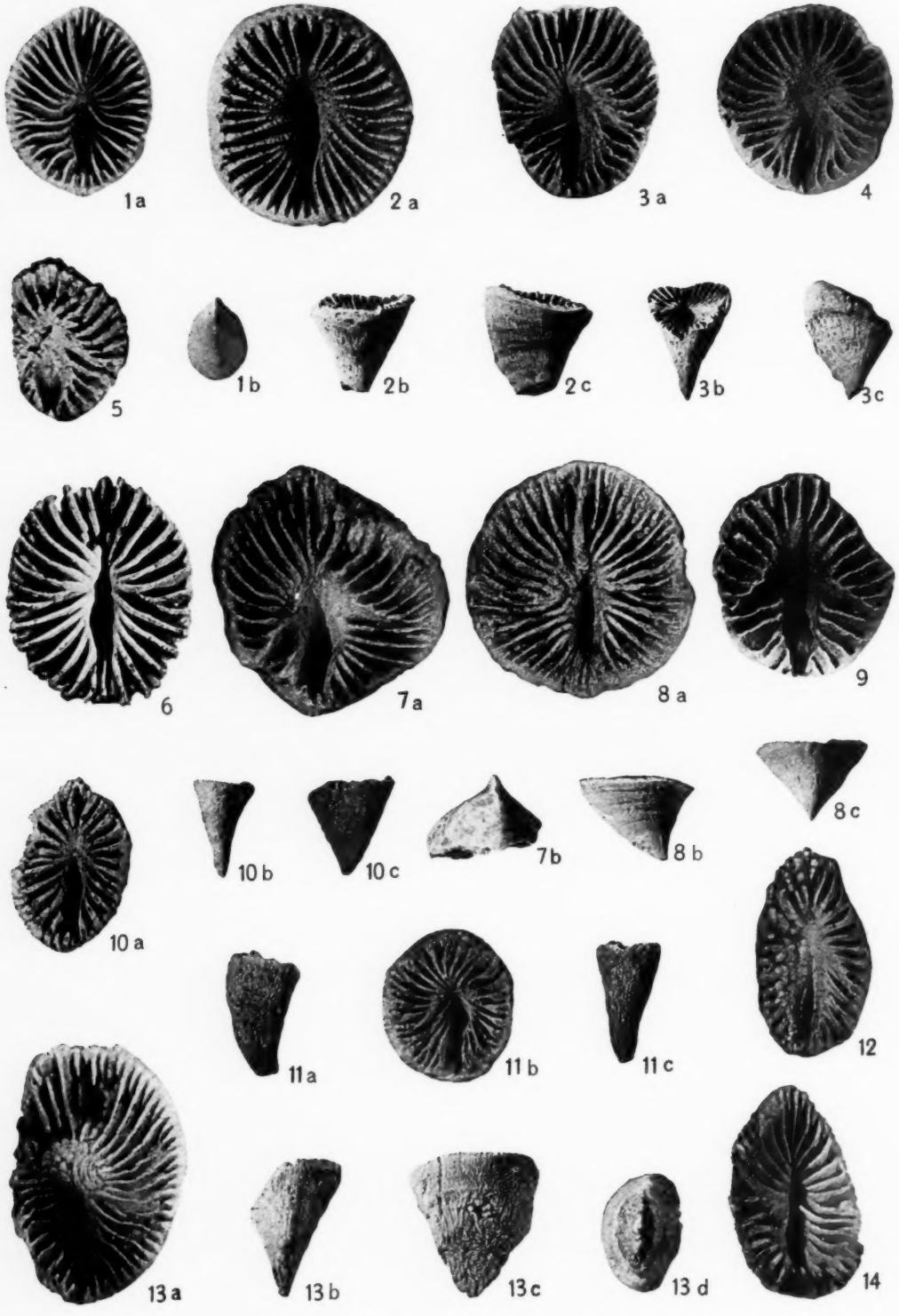
FIGS. *1–4, 6, 8–18*—*Triplophyllites* (*Homalophyllites*) *compressus* var. *lanceolatus* (Worthen), 1890. *1*, Calyx; approaches *T. clinatus;* USNM 115209a. *2*, Calyx in late maturity; AMNH 24006. *3*, Calyx; USNM 115208; approaches *T. clinatus*. *4*, Calyx; USNM 115208; approaches *T. clinatus*. *6a*, Calyx; *6b*, cardinal side; *6c*, left alar side; USNM 115212. *8a*, Cardinal side; *8b*, calyx; *8c*, left alar side; holotype of *Z. lanceolatus;* IGS (Worthen Coll.) 2572. *9a*, Cardinal side; *9b*, calyx; *9c*, left alar side; specimen less compressed than usual and more curved; USNM 37286. *10*, Calyx; USNM 115212. *11*, Calyx; AMNH 24003. *12*, Calyx in early maturity; AMNH 24004. *13*, Calyx in late youth; USNM 42878. *14*, Calyx in late youth; USNM 42878. *15*, Calyx in early maturity; USNM 42878. *16*, Calyx, AMNH 24005. *17*, Calyx; USNM 42878. *18a*, Cardinal edge; *18b*, right alar side; *18c*, calyx; USNM 115212. (p. 401)

5, 7, 19—*Triplophyllites* (*Homalophyllites*) *compressus* (Milne Edwards), 1857. *5a*, Calyx; "magnified"; from Milne Edwards; *5b*, lateral view of a specimen, probably not the same as *5a;* may actually be var. *lanceolatus;* "natural size"; from Milne Edwards; specimen lost. *7a*, Cardinal side; *7b*, calyx to match *5a; 7c*, right alar side; USNM 115202a. *19a*, Left alar side; *19b*, cardinal side; *19c*, calyx; USNM 37286. (p. 399)

20—Genus and species unknown. *20a*, Left alar side; *20b*, calyx, 1×; *20c*, cardinal side; USNM unnumbered specimen. (p. 402)



Easton, Mississippian cuneate corals



Easton, Mississippian cuneate corals

TRIPLOPHYLLITES (TRIPLOPHYLLITES) ELLIPTICUS (White), 1862

Plate 61, figures 1–5, 15; text-figures 6, 7

1865. *Zaphrentis elliptica* WHITE, Boston Soc. Nat. Hist. Proc., vol. 9, p. 31 (1862).
1883. *Zaphrentis elliptica*. WHITE, Twelfth Ann. Rept., U. S. Geol. Geog. Survey Terr. etc., pt. 1, p. 155, pl. 39, figs. 7a, b. (Not figs. 4a, b.) (Advance printing, 1880).
1889. *Zaphrentis carniatus* [sic]. MILLER, North American Geology and Palaeontology, p. 208. (*Nomen nudum* and/or misspelling).
1889. *Zaphrentis elliptica*. MILLER, N. Amer. Geol. and Palaeontology, p. 209.
1889. *Z. [aphrentis] elliptica*. ROWLEY, Amer. Geol., vol. 3, no. 2, p. 115.
1890. *Zaphrentis carinatus* WORTHEN, Geol. Survey Illinois, vol. 8, p. 75, pl. 10, figs. 3, 3a.
1890. *Zaphrentis carinata*. WORTHEN, Geol. Survey Illinois, vol. 8, expl. pl. 10.
1893. *Zaphrentis elliptica*. ROWLEY, Amer. Geol., vol. 12, no. 1, p. 50.
1894. *Zaphrentis elliptica*. KEYES, Missouri Geol. Survey, vol. 4, p. 111, pl. 13, figs. 6a, b.
1897. *Zaphrentis elliptica*. KEYES & ROWLEY, Iowa Acad. Sci., vol. 4, p. 30.
1898. *Zaphrentis carinatus*. WELLER, U. S. Geol. Survey Bull. 153, p. 645.
1898. *Zaphrentis elliptica*. WELLER, U. S. Geol. Survey Bull. 153, p. 647.
1905. *Zaphrentis elliptica*. MERRILL, U. S. Nat. Mus., Bull. 53, pt. 1, p. 703.
1908. *Zaphrentis elliptica*. ROWLEY, Missouri Bur. Mines, ser. 2, vol. 8, p. 38.
1918. *Zaphrentis carinata*. BUTTS, Kentucky Geol. Survey, Mississippian Formations of Western Kentucky, pp. 29, 41 (1917).
1922. *Zaphrentis carinata*. CUMINGS, Handbook of Indiana Geology: Indiana Dept. Cons., Pub. 21, pt. 4, p. 508.
1928. *Zaphrentis elliptica*. WELLER, Missouri Bur. Geol. Mines, ser. 2, vol. 22, pp. 187, 190, 199.
1930. *Triplophyllum carinatum*. CRONEIS, Arkansas Geol. Survey Bull. 3, p. 49.
1943. *Z. [aphrentis] elliptica*. SCHUCHERT, Stratigraphy of the Eastern and Central United States. John Wiley and Sons, Inc., New York, p. 684.

Description of holotype of Z. elliptica *White.*—Coral a curved cone with an elliptical cross-section. Epitheca (slightly eroded) with broad encircling swellings and faint interseptal grooves. Apical portion rather sharply carinate at cardinal and counter positions.

Calyx (diameters 14 by 18 mm.) with a broad smooth floor sloping into the cardinal fossula. Cardinal fossula narrow peripherally and expanded axially with walls of fused axial ends of septa and inner floor consisting of a tabula sloping about 30° into the fossula. Alar pseudofossulae indistinct. Major septa number 38. Cardinal septum becomes very short in upper portion of fossula but traverses lower portion and leans slightly to the right. Right cardinal quadrant with eight septa, right and left counter quadrants with ten septa, and left counter quadrant with eight septa. Counter septum slightly longer and thicker than adjacent majors. Minor septa absent. Tabulae smooth, sloping toward cardinal fossula and down toward epitheca elsewhere.

Description of paratypes.—A well preserved paratype (diameters 13.5 by 16 mm) has the calyx inclined 30° toward the cardinal position. Cardinal fossula almost T-shaped axially. Septa number 35. Cardinal septum slopes down into the cardinal fossula and crosses it at its base, leaning to

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EXPLANATION OF PLATE 60

Calyces 2×, lateral and apical views 1×.

FIGS. *1–6, 10—Triplophyllites* (*Triplophyllites*) *clinatus* (Greene), 1904. *1a*, Calyx; *1b*, apical view; USNM 115206a. *2a*, Calyx; *2b*, left alar side; *2c*, cardinal side; paratype; AMNH 24044. *3a*, Calyx; *3b*, cardinal side; *3c*, left alar side; holotype; AMNH 24041. *4*, Calyx; paratype; AMNH 24043. *5*, Calyx; hypotype; USC 408. *6*, Calyx; supposed syntype of *Z. capuliformis;* UI, RX 11B. *10a*, Calyx; *10b*, cardinal side; *10c*, left alar side; one of the syntypes of *Z. lanceolatus;* IGS (Worthen Coll.) 2572. (p. 395)

7–9—Triplophyllites (*Triplophyllites*) *clinatus* var. *capuliformis* (Rowley), 1900. *7a*, Calyx; *7b*, oblique view along the trace of the counter septum; paratype; UI, RX 11A. *8a*, Calyx; *8b*, left alar side; *8c*, cardinal side; holotype; UI, RX 11. *9*, Oblique view into calyx; paratype; UI, RX 11C. (p. 397)

11—Hapsiphyllum ulrichi (Worthen), 1890. *11a*, Left alar side; *11b*, calyx; *11c*, cardinal side; holotype; IGS (Worthen Coll.) 2573. (p. 390)

12–14—Triplophyllites (*Triplophyllites*) *clinatus* var. *bicarinatus* Easton, n. var. *12*, Calyx; paratype; USC 406. *13a*, Calyx; *13b*, cardinal side; *13c*, right alar side; *13d*, apical view; holotype; USC 280. *14*, Calyx; paratype; USC 279. (p. 396)

the left and lying in contact with the side of the counter septum. Right and left cardinal quadrants with six septa, one of these in each quadrant next to the cardinal septum being accidentally broken away at the calyx. Right counter quadrant with 11 majors, left counter quadrant with ten majors. Counter septum the same width as other septa, but longer, extending down the axial edge of the cardinal fossula as a ridge which overlaps the right side of the cardinal septum. Minor septa short, present only in counter quadrants. Alar pseudofossulae distinct.

Another paratype (diameters 11.5 by 14 mm.) has a narrow furrow at the inner end of the cardinal fossula, part of which furrow is occupied distally by the counter septum. Septa number 33. Right and left cardinal quadrants with five septa. Right counter quadrant with ten septa. Left counter quadrant with 11 septa. Counter septum longer than adjacent septa. All septa a trifle thickened except cardinal septum. Cardinal septum short leaning to left in floor of fossula. Alar pseudofossulae rather distinct. Minor septa absent.

A broken paratype shows the fibrous bundles of calcite in the septa inclined apically and axially at about 35°.

A paratype broken longitudinally in the cardinal-cardinal plane shows tabulae spaced 10 per cm., both complete and incomplete, peripherally recurved apically, and slightly irregular in spacing and strength. Dissepiments absent.

Dimensions.—Holotype: length, 25 mm. along alar septum.

Remarks.—White did not select a holotype for this species. The writer hereby selects the largest of his syntypes (UM 2084) figured herein (pl. 61, figs. 2 a–c) as the holotype.

This species seems to have been derived from *Neozaphrentis acuta* by completing the fusion of the septa bounding the lateral sides of the cardinal fossula, by increasing the size of the corallite and number of septa, by adding secondary septa, and by perfecting the cuneate tendency. This species is close enough to *Neozaphrentis* to give one an insight into the modifications which gave rise to at least one species group of *Triplophyllites*. The principal difficulty in the evolutionary picture concerns the general absence of dissepiments in this species. No dissepiments were observed in the syntypes, but a large specimen figured by section herein (pl. 61, fig. 15b) has a few dissepiments in late growth. It appears to the writer therefore, that the original concept of *Triplophyllites* must be changed somewhat so that the dissepiments should not be looked for principally in early stages of growth but should be expected to be developed according to the evolutionary stage represented by any particular species. Although this does not provide a sharp distinction between categories of corals, it seems to be all that can be said in the present state of our knowledge of North American corals of this genus. In recapitulation, it appears that the cuneate strain of *Triplophyllites* s.s. was derived from the non-dissepimented *Neozaphrentis acuta*. Advanced stages of *T. ellipticus* show true characters of *Triplophyllites* (such as are shown on pl. 61, figs. 15a, b, d.). Radiation from the type *ellipticus* could have given rise to *T. clinatus* and its relatives. Some of these possibly have dissepiments and others seemingly do not. One suspects that a polyphyletic group may be under consideration. The difficulty, of course, stems from lack of enough variable features to enable one to recognize supposed genetic strains. In any case, however, the species as considered herein are recognizable entities with stratigraphic usefulness. It is to be hoped that enough specimens may some day be collected to enable a student to make a detailed study of the ontogeny of these early *Triplophyllites* and to show patterns of change by percentages as in the case of *Z. delanouei* of Scotland,

In the interests of outlining philosophical problems raised by these particular species, I must point out that *T. ellipticus* as it exists in its types can logically be considered to be a related ancestor of *Clinophyllum*. The inclination of the calyx, nature of septal plan, and strength of the counter septum are quite in accord with this conjecture. On the contrary, the compression of the two groups is not in the same plane, so one cannot draw upon *T. ellipticus* as a near relative without interspersing intermediate forms which are not known to exist. More-

over, the stratigraphic distribution is wrong. More work needs to be done on the origin of *Clinophyllum*.

Description of the holotype of Z. carinata *Worthen.*—Corallite a curved and compressed cone, the apical region being somewhat flatter than the calical region. Epitheca smooth except for one deep depression near the calyx marking a period of rejuvenescence, and for several other faint encircling depressions. Calyx 8 mm. deep, ovate. Cardinal fossula narrow, deep, and located on the concave side of the corallite. Major septa number 32 or 33, there being about five in each cardinal quadrant and ten in each counter quadrant. The cardinal septum is very short. The counter septum is shorter than neighboring majors and lies in a shallow fossula.

Dimensions.—Length (incomplete) of cardinal side, 20 mm.; calical diameters 16 mm. by 13.5 mm.

Description of hypotypes.—Three specimens from Quarry, Iowa, have the external features of the species. One of these has been sectioned.

Section in early maturity (12 by 15 mm.).—Septa very much thickened by stereoplasm, the axial portion being a dark line. Loculi very narrow, with tabular intersections but no dissepiments observed. Cardinal septum very long, narrow, slightly swollen axially. Counter septum slightly thicker than adjacent majors. Alar pseudofossulae slightly wider than adjacent loculi. On one half of the section there are five septa in the cardinal quadrant and ten in the counter quadrant. Total septa probably 32. Minor septa absent.

Section in late maturity (diameters 14 by 17 mm.).—Septa slightly thickened by stereoplasm and with a dark axial line. Cardinal septum long, but discontinuous (probably with a central sag along its upper edge causing it to leave the plane of the section and then reenter it) and bent to the right. Cardinal fossula very much swollen axially. Counter septum half again as thick as adjacent septa. Six septa in each cardinal quadrant and 12 in each counter quadrant, total being 38. Septa are somewhat withdrawn from the axial region. Minor septa not observed. Tabulae in axis and between septa. Dissepimental intersections sparse. Alar pseudofossulae distinct.

At a slightly later stage minor septa appear and dissepiments are distinctly present. Septal retreat is more pronounced. Cardinal septum is shorter.

Localities.—15, 16, 17 (type locality), 18.

Occurrence.—This species occurs in the Maynes Creek member of the Hampton formation of Iowa and in the "Keokuk group" of Kentucky.

Material.—Specimens studied: 11. Syntypes, UM (White Coll.) No. 2084. Figured hypotype (this paper), USNM No. 115203A. White's figured hypotype, USNM 115203B. Unfigured hypotypes, USNM No. 115204.

TRIPLOPHYLLITES (TRIPLOPHYLLITES) CLINATUS (Greene), 1904

Plate 60, figures 1–6, 10; text-figure 9

1890. [*?Zaphrentis lanceolatus*]. WORTHEN, Illinois Geol. Survey, vol. 8, pl. 10, fig. 4b.
1904. *Zaphrentis clinatus* GREENE, Contributions to Indiana Palaeontology, pt. 19, p. 187, pl. 56, figs. 6–9.
1906. *Zaphrentis clinatus*. BEEDE, in Cumings and Beede, Indiana Dept. Geol. Nat. Res., 30th Ann. Rept., pp. 1204, 1373, pl. 11, figs. 1–1c.
1922. *Z.* [*aphrentis*] *clinatus*. CUMINGS, Handbook of Indiana Geology: Indiana Dept. Cons., Pub. 21, pt. 4, p. 505.

Description of holotype.—Corallite a modified elliptical cone curved in the direction of the cardinal fossula. The cross-section is tear drop shaped almost to the calyx, where it becomes ovate; the pointed edge of the tear drop cross-section follows the trace of the counter septum. The corallite is compressed more on the counter than on the cardinal side and has therefore one acute edge and one rounded edge. Theca with faint longitudinal markings.

Calyx shallow, 3 mm. deep at the inner edge of the fossula. Cardinal fossula deep, narrower at the ends than in the middle, flaring at the calyx floor. Alar pseudofossulae longer and slightly wider than other loculi. Counter fossula shallow, resulting only from the depression of the counter septum. Cardinal septum very short in the calyx but reaching the inner edge of the cardinal fossula at its floor and leaning to the right. Right and left cardinal quadrants with six major septa and no minors. Right and left counter quadrants with ten major

septa. Minor septa are best developed in the right counter quadrant; all are very short. Alar septa slightly higher than other septa in cardinal quadrants, and, therefore, extend onto the calyx floor. All 34 major septa meet to form the fossular wall. Tabulae not observed. Theca rather thick.

Dimensions.—Holotype 18.5 mm. high; calyx 14.5 mm. long and 12 mm. wide. One paratype's calyx is 14 mm. × 13 mm.; another is 16.5 mm. by 15 mm.

Paratypes.—The smallest paratype (calical diameters 8.5 mm.×11 mm.) has 31 major septa, no minor septa. Alar pseudofossulae are distinct.

The second paratype (diameters 13 mm.×14 mm.) has 33 major septa, a few minor septa in the counter quadrants, indistinct alar pseudofossulae, and a depression on the calical floor on the counter side of the cardinal fossula.

The largest paratype (diameters 15.5 mm.×16.5 mm.) has 33 major septa, minors in all but a few loculi, and fairly distinct alar pseudofossulae.

Material.—Specimens studied: 14. Holotype: AMNH Nos. 24042–24044. Hypotypes: USC Nos. 281, 408; syntype of *Z. lanceolatus* Worthen, 1890, pl. 10, fig. 4b: IGS (Worthen Coll.) No. 2573; USNM Nos. 115205, 115206, 115206a; UI (Rowley Coll.) No. RX 11B which is a syntype of *Z. capuliformis*.

Localities.—1, 3, 4, 5, 23?.

Occurrence.—The species is known with certainty from the Warsaw (Harrodsburg) and Salem limestones. It is known doubtfully from the lower Burlington limestones.

Remarks.—The syntypes of *Z. capuliformis* contain one specimen (UI No. RX 11B) which is a typical *T. clinatus*. The mode of preservation closely resembles that of corals from the Salem limestone at Lanesville and some other localities in Indiana. It is not at all like typical Burlington preservation. Although one cannot say definitely that it did not come from the lower Burlington limestone at Louisiana, Missouri, one certainly is prone to doubt it.

The calyx of this coral (diameters 13 by 16 mm.) has a long cardinal fossula extending two-thirds the calical diameter and is broadest about two-thirds of the length, tapering at both ends. Major septa total 32. Cardinal septum is a short ridge which only reaches the deepest part of the fossula. Cardinal quadrants each with six major septa and only rare indistinct minor septa. Counter quadrants each with nine major septa (the first of each being very short) and short minor septa. Counter septum shorter and lower than adjacent majors. The counter edge of the coral has a low sharp keel.

TRIPLOPHYLLITES (TRIPLOPHYLLITES) CLINATUS var. BICARINATUS Easton, n. var.

Plate 60, figures 12–14; text-figure 10

Diagnosis.—*Triplophyllites clinatus* with a keel centered at the position of the cardinal septum as well as having one at the position of the counter septum.

EXPLANATION OF PLATE 61

Calyces and sections 2× except as noted, lateral and apical views 1×.

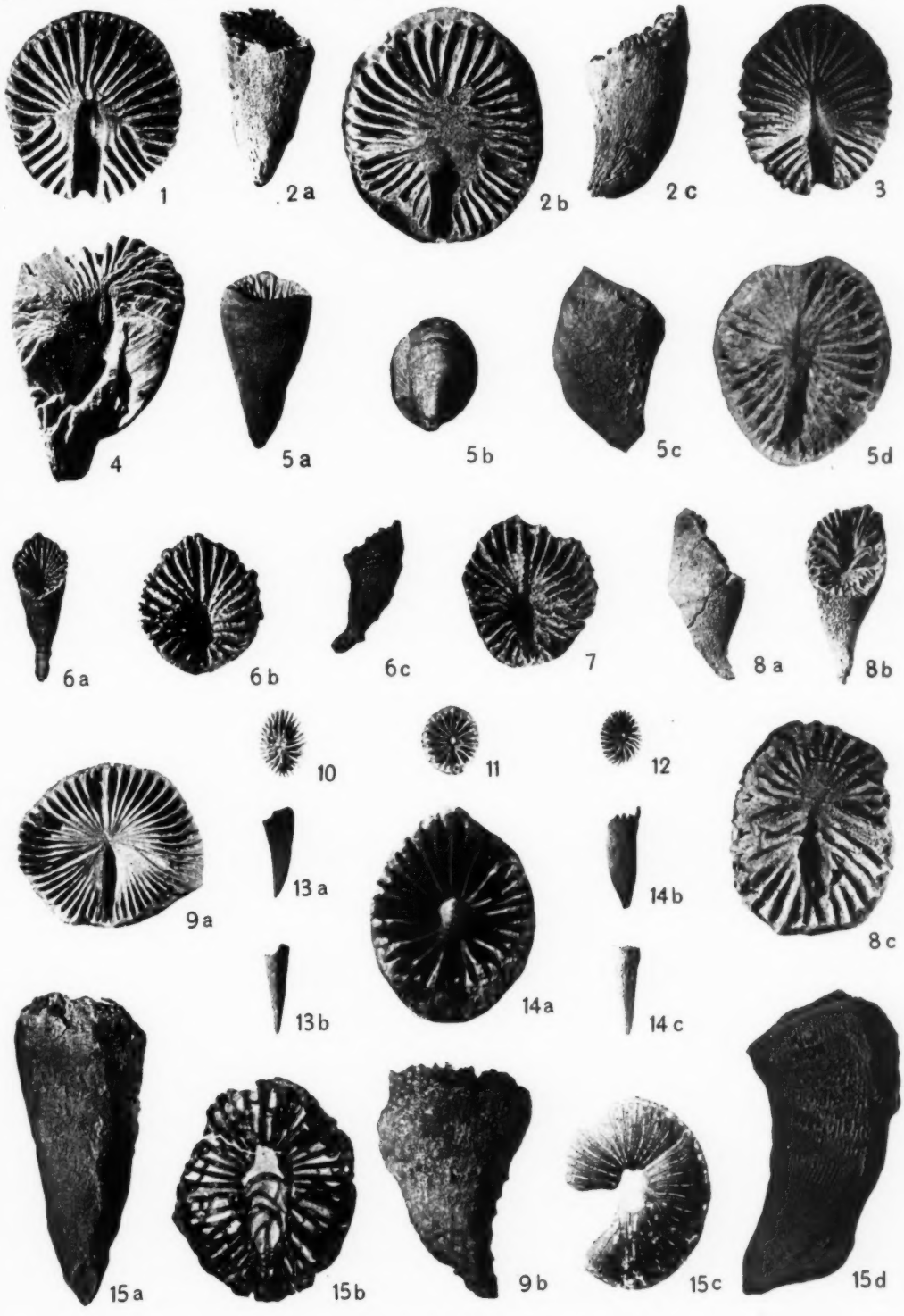
FIGS. *1–5, 15*—*Triplophyllites* (*Triplophyllites*) *ellipticus* (White), 1862. *1*, Calyx; paratype. *2a*, Cardinal side; *2b*, calyx; *2c*, right alar side; holotype. *3c* Calyx; paratype. *4*, Side view from broken right cardinal quadrant into interior, showing nature of septal fibers, 2×; paratype; figures *1–4* UM (White Coll.) 2084. *5a*, Cardinal side; *5b*, apical view; *5c*, left alar side; *5d*, calyx somewhat obscured by chert filling; holotype of *Z. carinata* Worthen; IGS (Worthen Coll.) 2564. *15a*, Cardinal side; *15b*, section in late maturity; *15c*, section in early maturity; *15d*, right alar side; hypotype; USNM 115203a; this specimen illustrates stages later than that present in the holotype. (p. 393)

6, 7—*Neozaphrentis acuta* (White & Whitfield), 1862. *6a*, Cardinal side; *6b*, calyx; *6c*, right alar side; holotype; AMNH 6366/1. *7*, Calyx; paratype; AMNH 6366/1. (p. 391)

8—*Triplophyllites* (*Homalophyllites*) sp. UA (Stoyanow Coll.) unnumbered. *8a*, Right alar side; *8b*, counter side; *8c*, calyx. (p. 399)

9—*Triplophyllites* (*Homalophyllites*) *reversus* (Worthen), 1890. *9a*, Calyx, 1×; *9b*, right alar side; holotype; IGS (Worthen Coll.) 2567. (p. 398)

10–14—*Cyathaxonia venusta* (Greene), 1904. *10*, Calyx; hypotype; AMNH 24045. *11*, Calyx; hypotype; AMNH 24046. *12*, Calyx; hypotype; AMNH 24047. *13a*, Left alar side; *13b*, cardinal side; hypotype; AMNH 24048. *14a*, Calyx, 6×; *14b*, right alar side; *14c*, cardinal side; holotype; AMNH 23412. (p. 388)



Easton, Mississippian cuneate corals

Description.—Holotype with faint longitudinal markings following the traces of the septa. Major septa 34 alternating with very short minors; five majors in each cardinal quadrant. Positions of a tabula are visible in the cardinal fossula. Alar pseudofossulae indistinct. Otherwise as in *T. clinatus.*

Dimensions.—Holotype: length, 21.5 mm. (incomplete); greatest diameter of calyx, 19 mm.; least diameter of calyx, 13 mm. (incomplete).

Comparison.—This variety differs from the typical form of the species in having two sharp edges due to compression, and in being compressed even at the calical rim.

Material.—Specimens studied: 17. Holotype, USC No. 280. Figured paratypes USC No. 279, 406. Unfigured paratypes, USC No. 282. Topotypes, USC No. 407. Figured hypotypes USC No. 408. Other specimens, USC No. 405.

Localities.—6, 7, 8.

Occurrence.—The type locality is near the base of the upper Warsaw (Harrodsburg) limestone (Meramecian series, Mississippian system) in an exposure about 4 feet high on the north side of highway 62, between the two quarries and the bridge over Little Indian Creek, between Corydon and Lanesville, Indiana.

Remarks.—This variety grades into typical *T. clinatus.*

TRIPLOPHYLLITES (TRIPLOPHYLLITES) CLINATUS var. CAPULIFORMIS (Rowley), 1900

Plate 60, figures 7–9; text-figure 8

1900. *Zaphrentis capuliformis* ROWLEY, Amer. Geol., vol. 25, no. 5, p. 270, pl. 5, figs. 67–70. (in part).

1908. *Zaphrentis capuliformis.* ROWLEY, Missouri Bur. Geol. Mines, ser. 2, vol. 8, p. 38.

Description of holotype.—Corallite (UI No. RX 11) a simple short, flaring, cone, curved toward the cardinal fossula and with an elliptical cross-section. The keel at the counter position is weakly developed. Epitheca with faint encircling striae and a few indistinct encircling constrictions. Calyx (diameters 16.5 by 17.5 mm.) 3 mm. deep with a broad floor developed on the axial portions of the septa. Cardinal fossula deep, narrower at its midlength than at either end, and bounded laterally by the fused ends of septa. Cardinal septum indistinct. Major septa total 36. Right and left cardinal quadrants with six major septa of which the first on either side of the cardinal septum is indistinct. Right counter quadrant with 11 major septa of which the first adjacent to each alar pseudofossula is very short. Counter septum axially swollen and longer and little higher than adjacent majors which converge pinnately toward it. Alar pseudofossulae prominent but narrow. Minor septa as septal ridges. Tabulae presumably are responsible for the floor of the cardinal fossula. Dissepiments possibly present in right counter quadrant.

A paratype (UI RX 11A) (diameters 17 by 18.5 mm. incomplete) has eight majors in the right cardinal quadrant and 11 in each of the counter quadrants. The left cardinal quadrant is obliterated. The counter septum is longer and higher than the adjacent pinnately arranged majors, but is not axially swollen. Minor septa are short. Perhaps the calyx originally contained 40 major septa. The counter edge of the coral is produced into a prominent ridge-like keel.

Another paratype (UI No. RX 11C) (diameters 13.5 by 15 mm.) has six majors in each cardinal quadrant and nine in each counter quadrant. The counter septum is longer and higher than the adjacent pinnately arranged majors and is axially swollen. Major septa total 32.

Dimensions.—Holotype: 11 mm. high; alar septum 15 mm. long.

Material.—Specimens studied: 3. UI (Rowley collection). Holotype: (Rowley, 1900, pl. 5, figs. 67, 68) RX 11. Largest paratype (Rowley, 1900, pl. 5, figs. 69, 70). RX 11A. Poorest paratype: RX 11C.

Occurrence.—Localities: 23 (type locality), 24.

Remarks.—Rowley did not designate a holotype but he did mention (Rowley, 1900, p. 273) that figs. 67, 68 of his plate 5 represented views of "one of the types." This specimen which he figured, which is University of Illinois (Rowley collection) No. RX 11, is hereby designated the holotype. The other three specimens, which he may or may not have intended to be syntypes, become paratypes. One of these

(UI, RX 11B) is described under *T. clinatus* instead of with the other types.

The dissepiments mentioned in the description of the holotype are a few blister-like swellings on the calical walls. It cannot be said that they are definitely dissepiments without sectioning them; this operation was not done.

This variety of *T. clinatus* contains enough variation among the types to show how modifications gave rise to the typical form. By comparing the figures, one can observe the *T. clinatus* trend going from the holotype (RX 11) to the two paratypes (first RX 11A and then RX 11C).

Rowley's figures of the calices are largely based on presumption. The writer cleaned considerable matrix out of all the specimens in order to reveal their characters.

I do not find any ridge on the cardinal side of the corals, which Rowley said was more or less distinct. At best the corals are only sharply rounded there as a result of their having elliptical cross-sections.

Mature specimens of this variety may be distinguished from the typical form by having a more widely flaring shape, more numerous septa, and a thinner epitheca. Otherwise they are quite similar.

Subgenus HOMALOPHYLLITES Easton, 1944 emended

Diagnosis.—Triplophyllites with the cardinal fossula on the convex side of the corallite.

Type.—Lophophyllum calceola White and Whitfield, 1862.

Remarks.—Previously the writer (Easton, 1944, p. 42) revised the concept of *Hapsiphyllum* Simpson, 1900 to include corals with the features of *Lophophyllum calceola*. The subgenera *Hapsiphyllum* and *Homalophyllites* were established at the same time. Although that seemed to provide an orderly systematic arrangement at that time, it is not found to be satisfactory now. The writer subsequently has seen many specimens of corals similar to *L. calceola* and *Hapsiphyllum calcariforme* in new species to be described or redescribed in the future. It is concluded that the subgenus *Homalophyllites* should be separated from the genus *Hapsiphyllum* and assigned to the genus *Triplophyllites*.

If *Zaphrentoides* should be proved to be the same as *Triplophyllites* then the subgenus *Zaphrentoides* can be used to replace *Homalophyllites* of this paper. This would revive the taxonomic category established by Schindewolf in 1938 for the particular corals with the cardinal fossula on the convex side of the corallite. It would not, however, revive Schindewolf's usage of the subgenus *Hapsiphyllum*.

Corals with circular cross-sections, cuneate, and calceolid shapes occur in this subgenus. Species groups are established to segregate the three categories.

Homalophyllites calceolus species group

Diagnosis.—Homalophyllites with a calceolid shape.

Remarks.—Lophophyllum calceola White and Whitfield, 1862 belongs here.

Homalophyllites reversus species group

Diagnosis.—Homalophyllites with a circular cross-section.

Remarks.—The writer (Easton, 1944, p. 39) once theorized that *Z. reversa* Worthen, 1890 might warrant the separation of *Triplophyllites* into subgenera on the basis of location of the cardinal fossula with respect to curvature. At that time *Z. reversa* had not been figured and so was poorly known. It and other corals considered herein are known now to fit the requirement formerly stated for the recognition of the atypical subgenus. *Z. reversa*, however, is not a suitable type for reasons stated below.

TRIPLOPHYLLITES (HOMALOPHYLLITES) REVERSUS (Worthen), 1890

Plate 61, figures 9a, b

1889. *Zaphrentis reversa* MILLER, North American Geology and Palaeontology, p. 210. (nomen nudum).
1890. *Zaphrentis reversa* WORTHEN, Geol. Survey Illinois, vol. 8, p. 78.
1898. *Zaphrentis reversa*. WELLER, U. S. Geol. Survey Bull. 153, p. 648.

Description of holotype.—Coral a curved cone with an apical angle of 40–45°. Theca with short spines arranged more or less in concentric bands, with broad undulations of growth, and with faint longitudinal striations. Calyx moderately deep (9 mm. deep

to floor of calyx). Cardinal fossula deep, on the convex side of the corallites, extending to the center of the calyx, and widest about ⅓ of the way to the center. Alar pseudofossulae prominent. Major septa number 49, and most of them extend across the calical floor. Cardinal septum extends straight across the cardinal fossula at its floor but is very short above the fossular floor. Right and left cardinal quadrants each contain ten septa, of which the alar septa are slightly more robust than the others. Right counter quadrant contains 14 majors. The counter septum is slightly more robust and is slightly higher than its neighbors. In the left counter quadrant, the seventh and thirteenth septa (counting clockwise) are aborted and their positions are marked by extra wide loculi.

Material.—Specimens studied: 1. Holotype and only known specimen, IGS (Worthen Collection) No. 2567.

Type locality.—Warsaw beds, near Columbia, Monroe Co., Illinois.

Locality.—14 (type locality).

Remarks.—Only one specimen of the species is known, although numerous paleontologists have collected from beds of Warsaw age. Under the circumstances, the specimen may be merely a sport. Moreover, the specimen is known to be aberrant in the abortion of the seventh and thirteenth septa of the left counter quadrant. Not only are these septa reduced to ridges, but their allotted position near the axis has been taken over by adjacent septa. This indicates that the shortening of the two septa took place during the earlier ontogeny of the creature. In view of these things, it may be that the species group may contain only this one species among American Mississippian corals.

T. reversus has not been figured previously, probably because extensive preparation was necessary before the calyx was cleaned of matrix.

Homalophyllites compressus species group

Diagnosis.—*Homalophyllites* with a cuneate shape.

Remarks.—*Zaphrentis compressa*, *Z. lanceolata* and an undescribed species from Arizona belong here.

TRIPLOPHYLLITES (HOMALOPHYLLITES) sp.
Plate 61, figures 8 a–c; text-figure 12

Remarks.—The specimen discussed below was very kindly lent by Dr. Alexander Stoyanow from his collection. The species will be described by Dr. Stoyanow in a forthcoming article on the index fossils of Arizona, but he has graciously consented to the publication of this statement so that all of the cuneate corals known to the writer may be included in this paper.

The specimen is slightly cuneate and has the cardinal fossula on the convex side of the coral. It is similar to *T.* (*T.*) *ellipticus* in most respects except for location of the cardinal fossula with respect to curvature. It also resembles *Clinophyllum* except that the inclination of tabulae and location of cardinal fossula are reversed with regard to curvature. In the course of time the phylogenetic relationships of *Clinophyllum* to *Triplophyllites* should be studied critically when enough species and specimens allied to this specimen from the Escabrosa limestone are known.

TRIPLOPHYLLITES (HOMALOPHYLLITES) COMPRESSUS (Milne-Edwards), 1857
Plate 59, figures 5, 7, 19; text-fig. 5

1857. *Zaphrentis compressa* MILNE-EDWARDS, Histoire Naturelle des Coralliaires ou Polypes Proprement Dits, Atlas, pl. G1, fig. 3.
1860. *Zaphrentis compressa*. MILNE-EDWARDS, Histoire Naturelle des Coralliaires ou Polypes Proprement Dits, vol. 3, p. 342.
1876. not *Zaphrentis compressa* ROMINGER, Geol. Survey Michigan, vol. 3, pt. 2, p. 151, pl. 52 [=*Z. davisana* Miller, 1889, p. 209].
1889. *Zaphrentis compressa*. MILLER, N. Amer. Geol. and Palaeontology, p. 208.
1898. *Zaphrentis compressa*. WELLER, U. S. Geol. Survey Bull. 153, p. 646.
1904. *Zaphrentis compressa*. GREENE, Contributions to Indiana Palaeontology, pt. 18, p. 177, pl. 52, figs. 8–11.
1906. *Zaphrentis compressa*. BEEDE, in Cumings and Beede, Indiana Dept. Geol. Nat. Res., 30th Ann. Rept., pp. 1204, 1373, pl. 7, figs. 4–4d.
1922. *Triplophyllum compressa*. BUTTS, Kentucky Geol. Survey, ser. 6, vol. 7, pp. 110, 112–116.
1922. *Zaphrentis compressus*. CUMINGS, Handbook of Indiana Geology, Indiana Dept. Cons., Pub. 21, pt. 4, p. 505.
1930. *Zaphrentis compressa*. MORSE, Mississippi Geol. Survey Bull. 23, p. 110.

1943. *Triplophyllum compressa.* McFARLAN, Geology of Kentucky, p. 75.
1943. *Triplophyllum compressum.* SCHUCHERT, Stratigraphy of the Eastern and Central United States. John Wiley and Sons, Inc., New York, p. 531.
1943. *Z. [aphrentis] compressa.* SCHUCHERT, Stratigraphy of the Eastern and Central United States. John Wiley and Sons, Inc., New York, p. 591.

Translation of Original Description

Corallite strongly compressed, cuneiform, narrow, pointed at the bottom, straight or scarcely curved in the direction of the large axis of the calyx. Growth lines very little developed. Calyx elliptical, of which the little axis amounts to nearly half the large axis. The uppermost tabula is only flat at the axis for a short distance. The oblong septal [cardinal] fossula is well developed and very deep, located on the side of large curvature. Septa 22, subequal, strong, a little thickened in their outer half, well developed, straight, and alternating with an equal number of very small septa. Height of corallite, 2½ centimeters; large axis of the calyx at least 1 centimeter.

Carboniferous formation: Spurgen [sic] Hill (Indiana).

We consider as a variety of this species a corallite, (pl. G1, fig. 4) from the same locality, which is much shorter and wider than the specimens previously described, the uppermost tabula of which is flat for a greater extent, and in which there are 30-odd major septa.

Remarks.—Milne-Edwards figured only one of the species referred to above. These figures are reproduced herein. The unnamed variety of this species, which he mentioned in the text as being figure 4 on plate G1, does not appear there or elsewhere in the Atlas, nor is it mentioned in the legends accompanying the figures.

All efforts to locate the type specimens have been unavailing. Although Milne-Edwards states (1860, p. 342) that the specimens were discovered by Casseday, he does not say what disposal was made of them. M. Ranson, of the Museum d'Histoire Naturelle in Paris assures me that they are not there. Casseday's collection is missing, but rumor has it that some of it, at least, was at the St. Louis Academy of Sciences for a time.

Lacking the types, the writer has selected a specimen as principal hypotype (USNM No. 37286) which agrees very closely with the best figure given by Milne-Edwards (1857 (Atlas), pl. G1, fig. 3b). M. Ranson has pointed out to the writer that there is good reason to believe that figures 3 b and 3a in the work just referred to are actually different specimens. The explanation of the plates in that work frequently distinguishes between two views of the same specimen, as opposed to views of different specimens. Inasmuch as a definite statement such as "Calice du même, grossie" is lacking and one only finds "Calice grossi," the evidence is strong that Milne-Edwards had two specimens before him.

A further problem concerns on which side of the specimen the cardinal fossula is located. The figures do not help one to decide. The description says merely that the fossula is on the side of "la grande courbure." If one understands this to mean the most curved side, then the connotation is of greatest radius of curvature and the fossula would be on the concave side when viewed from an alar side. If one understands Milne-Edwards to have indicated a side with a long arc as opposed to a side with a short arc, then the fossula would be on the convex side. Fortunately, Milne-Edwards (and his colleague Haime) were singly and collectively consistent in their usage of the particular phraseology. By checking descriptions of species whose location of cardinal fossulae is known and by comparing illustrations with accompanying descriptions of other species, one can demonstrate to one's own satisfaction that "la grande courbure" means the convex side when viewed from an alar side.

Having eventually discovered what *Zaphrentis compressa* is like, the writer selected a specimen which agrees very closely with figure 3b of Milne-Edwards. This (largest) specimen, from the same locality, is described below as a hypotype.

Description of hypotypes of Homalophyllites compressa.—Largest specimen narrowly elliptical throughout, straight. Epitheca somewhat eroded showing septal traces. Calyx with very prominent elongate cardinal fossula whose floor slopes down steeply from the slightly sloping smooth calical floor. Cardinal septum short at distal end but reaching across fossula proximally and slightly bent to the right. Counter septum slightly longer than other majors. Cardinal quadrants each contain four major septa. Counter quadrants each contain seven major septa. Total major septa,

therefore, number 24. Minor septa intercalated between some major septa. Alar pseudofossulae very weakly developed. Length, 25 mm.; calical diameters, 7 by 11 mm.

Three specimens are distinctly curved. In each, the cardinal fossula is on the convex side. Several specimens show the epitheca to have been smooth except for occasional encircling furrows. Some specimens may expand, then diminish their diameter, and expand again. In such instances, that portion including the latter expansion is usually less compressed than the rest of the calyx. The counter septum may be long, short, thick, thin, in a faint fossula, or lacking fossular expression. As variable as it is, it is curious that something usually distinguishes it in single or combined form from the preceding list.

Material.—Specimens studied: ten. Figured hypotypes: USNM No. 37286. Other hypotypes, USNM Nos. 115202, 115202a. Other specimens: USNM No. 115211.

Localities.—6, 10, 11.

Occurrence.—*T. (H.) compressus* occurs in the Salem limestone.

TRIPLOPHYLLITES (HOMALOPHYLLITES) COMPRESSUS var. LANCEOLATUS (Worthen), 1890

Plate 59, figures 1–4, 6, 8–18; text-figure 4

1889. *Zaphrentis lanceolata* MILLER, North American Geology and Palaeontology, p. 209 (nomen nudum).
1890. *Zaphrentis lanceolatus* WORTHEN, Geol. Survey Illinois, vol. 8, p. 76, pl. 10, figs. 4, 4a (in part).
1890. *Zaphrentis lanceolata.* WORTHEN, Geol. Survey Illinois, vol. 8, expl. pl. 10.
1898. *Zaphrentis lanceolata.* WELLER, U. S. Geol. Survey Bull. 153, p. 648.
1926. *Triplophyllum (Zaphrentis) compressa.* BUTTS, Geol. Survey Alabama, Spec. Rept. 14, p. 173.
1926. *Zaphrentis compressa.* BUTTS, Geol. Survey Alabama, Spec. Rept. 14, p. 56, figs. 6, 7.

Description of holotype of Zaphrentis lanceolatus *Worthen, 1890.*—Corallite in the form of an elliptical cone with slight obliquity toward the cardinal fossula. The cross-section changes from the apex so that in the proximal portion the cross-section is a narrow ellipse, but in the distal portion it becomes less excentric, and, therefore, is broadly elliptical at the calyx rim. Theca smooth except for faint encircling wrinkles.

Calyx shallow (about 3 mm. deep) and with the septa everted about 1 mm. beyond the thecal rim. The outer fourth of each major septum slopes down abruptly to the theca but gradually to the calyx floor. Cardinal fossula deep, narrow, and parallel-sided in the inner half. Alar pseudofossulae not differentiated but the position of the alar septum can be approximated by the slight bunching together of septa into four groups. Cardinal septum reaches almost to the axis in the floor of the fossula and is directed slightly to the left (when the cardinal fossula is orientated downward). In the calyx the cardinal septum extends about one-third the radius. Counter septum is a trifle longer and higher than the other majors near the axis, but is entirely similar to them near the theca. The calyx contains 22 major septa distributed as follows: the cardinal septum, four in each cardinal quadrant, six in each counter quadrant, and the counter septum. Short minor septa are distributed alternately with the majors. The minor septum on either side of the cardinal septum is longer than the other minors in the lower portion of the fossula and fuses with the next major septum at the fossular wall. These two minor septa are presumably short primary septa, whereas the other minors are secondary septa. Major septa coalesce axially to form a sloping calical floor of stereom. Tabulae were not observed, unless the floor of the fossula is a tabula.

Dimensions.—Height: 21 mm. Long dimension of calyx: 10 mm. Short dimension of calyx: 9 mm.

Localities.—1, 5, 6, 9, 10, 19 (type locality), 13, 20, 21, 25.

Material.—Specimens studied: 64. Holotype: IGS (Worthen collection) No. 2572. Other material: AMNH Nos. 24003–24006 (Greene's figured hypotypes of *Zaphrentis compressa*); USNM No. 71629 (Butt's figured hypotype of *Zaphrentis compressa*), 50771, 42878, 41229, 115207–115210.

Remarks.—Worthen left two syntypes of this species. One of these, which fits his measurements of an "average size specimen" and which he figured on pl. 10, figs. 4, 4a, is here designated the holotype.

The other syntype was figured on pl. 10, fig. 4b, but there is no mention of this figure

in the text or in the explanation of plate 10. The measurements of the specimen fit the two recognizable dimensions of the figure but do not correspond to the measurements given on p. 76 for the "Broadest specimen." Perhaps Worthen took his measurements from the plate and not from the specimen. The specimen is referred in this report to *Triplophyllites clinatus*.

Worthen reports the type locality as "Warsaw beds of the St. Louis group, Spergen Hill, Indiana, and Coalsburg [sic], Ky." The famous collecting locality at Spergen Hill is in the Salem limestone (Iowan series of the Mississippian). There is no Salem limestone around Colesburg, but a good section of the underlying Warsaw limestone and shale is present from which collectors have obtained good faunas through the years. The label accompanying the syntypes reads only "Warsaw beds Coalsburg [sic], Kentucky," hence, this affords presumptive evidence that the syntypes are from the Warsaw formation at Colesburg, Kentucky.

Other specimens before the writer were collected by Greene and constitute the hypotypes to substantiate his identification of *Zaphrentis compressa*. Their label reports them to be from Lanesville, Spergen Hill, and Georgetown, all in Indiana. The first two of these references and probably the third constitute occurrences in the Salem limestones, but one cannot decide which of his specimens came from what locality.

In summation, then, this variety appears to occur in the Warsaw formation and Salem limestone.

The location of the cardinal fossula with respect to curvature is variable in this variety. Most specimens are simply straight cones and so have no convex or concave side. Some other specimens are very slightly curved in the apical portions only, in which cases one finds some specimens to have the fossula on the convex side and others to have it on the concave side. Of the 48 specimens before me which should afford evidence, the location of the fossula with regard to curvature cannot be decided for 32 specimens; is on the concave side of five specimens; and is on the convex side of 11 specimens.

INCERTAE SEDIS

Gen. nov. et sp. nov.

Plate 59, figures 20a–c; text-figure 13

Description.—Corallite simple, large, cuneate. Epitheca eroded to show septal traces, otherwise with only faint broad incircling swellings. Calyx with central depression floored by a tabula on whose surface are septal traces. Cardinal septum very short. Right cardinal quadrant with ten major septa; right counter quadrant with 16 major septa; counter septum joined on either side by contratingent minor septa; left counter quadrant with 20 major septa; left cardinal quadrant with eight major septa; total major septa—56. Minor septa short and contratingent with the major septa. The major septa of the cardinal quadrant are pinnately arranged around the cardinal fossula. Tabulae depressed proximally at the axial region and at their periphery, but bent upward about half the distance from the axis to the periphery.

Dissepiments in as many as two (and possibly more) ranges distally, but seemingly absent proximally. Six dissepiments occur in 1 cm.

Length, 54 mm. Calical diameters, 8 mm. by 28 mm.

Locality.—5.

Material.—Specimens studied: one. This specimen, which carried no number, is in the systematic collections of the U. S. National Museum.

Remarks.—The writer knows of no other coral like this. It combines features of *Triplophyllites* and *Hapsiphyllum* but cannot be referred to either genus as now defined.

LOCALITY LIST

Information as to localities and stratigraphy of specimens not collected by the writer is given as it appeared on the labels. The writer's interpretation of the stratigraphy for all localities is given in terms of present usage in brackets. For pertinent discussions of the vicissitudes of stratigraphic usage see Cumings, 1922; Stockdale, 1929; and Stockdale, 1939.

1. Colesburg, Kentucky. Warsaw beds. [Muldraugh formation—upper Harrodsburg limestone.]

2. Colesburg, Kentucky. Warsaw-Somerset beds. [Muldraugh formation—base of Salem limestone.]
3. West Point, Kentucky. Salem (Spergen) limestone. (One label reads "Keok. group.") [Salem limestone.]
4. Edwardsville, Indiana. Warsaw stage. [Edwardsville division—upper Harrodsburg limestone.]
5. Lanesville, Indiana. Salem (Spergen) limestone. [Salem limestone.]
6. Spergen Hill, Indiana. Salem (Spergen) limestone. [Salem limestone.]
7. Abandoned quarry 0.2 mi. east of bridge over creek 2.4 mi. north of intersection of 5th and M Streets, Bedford, Indiana. (NE ¼, NW ¼, sec. 2, T. 5 N., R. 1 W.) [Base of lower Harrodsburg limestone.]
8. Road cut about 4′ high on north side of highway 62, between two quarries and bridge over Little Indian Creek, about 1.9 mi. W. of the west edge of Lanesville, Indiana. SE ¼, sec. 25, T. 3 S., R. 4 E. [Near top of upper Harrodsburg limestone.]
9. Clarksville, Tennessee. Warsaw. 10–20′ level. [Warsaw formation?]
10. Clarksville, Tennessee. Warsaw, 25–30′ level. [Warsaw formation?]
11. Lawrence Co., Indiana [Salem limestone?]
12. Warsaw formation, St. Louis stage, Mississippian period. Georgetown and Lanesville, Harrison Co., Indiana. [Salem limestone.]
13. Warsaw formation, St. Louis stage, Mississippian period. Lanesville, Harrison Co., Indiana. [Salem limestone.]
14. Warsaw beds. Near Columbia, Monroe Co., Illinois. [Warsaw formation.]
15. Keokuk limestone, Bentonsport, Iowa. [Keokuk limestone.]
16. Maynes Creek member of the Hampton formation. Quarry, Marshall Co., Iowa. [Maynes Creek member.]
17. Base of Burlington limestone, Burlington, Iowa. [Burlington limestone.]
18. Keokuk group, Colesburg, Kentucky. [Borden group.]
19. Lanesville, Spergen Hill, and Georgetown, Indiana. Warsaw formation, St. Louis stage, Mississippian period. [Salem limestone.]
20. Fort Payne chert. Florence, Lauderdale Co., Alabama. [Fort Payne formation.]
21. Warsaw. First R.R. bridge S. of Colesburg, Kentucky. [Muldraugh formation.]
22. Kinderhook group. Burlington, Iowa. [Kinderhook group and possibly lowest Osage group.]
23. Fifth division of the Burlington limestone of Rowley's classification, Louisiana, Mo. [Probably the base of the upper Burlington limestone.]
24. Fourth lower Burlington division of Rowley's classification, Louisiana, Mo. [Top of the lower Burlington limestone.]
25. West face of easternmost of two quarries on Highway 62 about 6.5 miles east of intersection of Chestnut and Market Streets in Corydon, Indiana. [Basal 10 feet of Salem limestone.]

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JOURNAL OF PALEONTOLOGY, VOL. 25, NO. 3, PP. 405–407, PL. 62, MAY 1951

A LOWER CAMBRIAN FOSSIL LOCALITY NEAR ADDY, WASHINGTON

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IN THE summer of 1949, while working for the Geological Survey of Canada in southeastern British Columbia, the writer had occasion to visit several fossil localities in the adjacent Metaline Falls and Stevens counties of Washington. Of particular interest were the outcrops of fossiliferous Lower Cambrian rocks containing pleosponges, brachiopods, and trilobites. Abundant pleosponges were collected from the Old Dominion limestone near Colville and the nameless limestone band occurring near the base of the Maitlen phyllite in the Metaline quadrangle. Olenellid trilobite fragments and brachiopods were collected from the Addy quartzite near the town of Addy in Stevens County. Because it is the writer's intention to describe the pleosponge localities and fossils in greater detail in a separate paper at a later date, only the Addy fossils will be described here. It is a pleasant duty to express sincere gratitude to Mr. J. P. Thomson of Colville, who went out of his way to acquaint the writer with the geology of Stevens County, and without whose help it would have been impossible to make the large fossil collections in the time available.

The exact position of the Addy fossil locality is at the south end of a low ridge almost opposite the town of Addy on the west side of Colville River in the SW ¼, Sec. 13, T 33 N, R 39 E. The fossils occur in a reddish flaggy quartzite and argillaceous quartzite. A short distance north the Addy quartzite is overlain by the old Dominion limestone. The locality was previously mentioned by Branson (1931), who reported the presence of *Kutorgina cingulata* (Billings) and a few fragments of trilobites. Resser (1934, p. 7) mentioned the same locality. The writer collected the following fossils from the locality:

Micromitra (*Paterina*) sp.
Kutorgina cf. *cingulata* (Billings)
Kutorgina sp.
Rustella cf. *edsoni* Walcott
Hyolithellus sp.
Nevadia addyensis n.sp.
numerous olenellid fragments
fucoids.

The fauna is undoubtedly Lower Cambrian in age; and the presence of the rare genus *Nevadia*, with its very primitive characteristics, suggests the lower portion of the Lower Cambrian.

The writer has collected pleosponges in the overlying Old Dominion limestone, as have several others before him, while Dr. Bennett has found a specimen of *Wanneria*. The Old Dominion limestone is, therefore, also Lower Cambrian in age.

In the adjacent Metaline Quadrangle, Park and Cannon (1943) reported that poorly preserved fragments of Cambrian trilobites were found in the Gypsy quartzite. Dr. Little, of the Geological Survey of Canada, and the writer collected abundant pleosponges in the limestone band near the base of the Maitlen phyllite overlying the Gypsy quartzite. It is the writer's opinion that the Gypsy quartzite is equivalent in age to the Addy quartzite, and that the lower portion of the Maitlen phyllite is equivalent in age to the Old Dominion limestone. Tracing the outcrops of the Gypsy quartzite northward across the international boundary it is obvious that the same quartzitic beds were called the Reno and Quartzite Range formations in the Salmo area of British Columbia, and that farther north the same quartzitic rock unit was called the Hamill series. However, since no fossils were found in the Hamill series it is apparently late Pre-Cambrian in age (Okulitch, 1949).

The fossils collected in the Addy quartzite are preserved as deep impressions in the

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rock. The preservation of the brachiopods and *Hyolithellus* is not sufficiently good for dependable specific determinations. The two cephalons and several smaller fragments of *Nevadia*, however, are unmistakable and permit establishment of a new species. The genus *Nevadia* was originally described by Walcott (1910) from the Lower Cambrian of Nevada and regarded by him as the most primitive of the Olenellidae. The original specimen was thought to be characteristic of a fossil zone considerably below the *Olenellus* zone. Later work by Poulsen (1932) and by Raw (1936, 1937) indicates that the *Nevadia* zone overlaps the *Callavia-Olenellus* zone. *Nevadia* and its subgenus *Nevadella* are easily distinguished from all other Olenellidae by their forward-tapering conical glabellae.

NEVADIA ADDYENSIS Okulitch, n. sp.
Plate 62, figures 1, 2

The holotype is an almost complete cephalon, with attached genal spines. The greatest width is 47 mm. and the length 21 mm. In overall shape it is a slightly flattened semicircle. The convexity is slight, but the glabella and palpebral lobes stand above the general surface.

Glabella is long and narrow, tapering towards the front. It is separated by a narrow preglabellar area from the marginal furrow. The anterior border or rim is relatively narrow and of uniform width. The frontal lobe of the glabella is very narrow and long. The four glabellar furrows are shallow and slope from each side backwards towards the center. Glabellar furrows are apparently not connected across the glabella. The occipital ring is strong and stands somewhat higher than the glabella. There is a faint indication of an occipital node. The posterior margin of the cephalon slants gently backwards from the occipital ring to the base of the genal spine. The genal spine is slender, slightly curving, and about equals the glabella in length.

The palpebral lobes are long and narrow and extend from the frontal lobe, to opposite the fourth glabellar furrow. At the front the palpebral lobe is apparently connected with the back portion of the frontal lobe. However, the dorsal furrow is visible all the way around the glabella. The palpebral lobes are very close and nearly parallel to the glabella. Facial suture is not visible.

The species differs from *Nevadia weeksi* Walcott by having a longer and narrower glabella with a more pronounced forward taper. The preglabellar area is much narrower than in *N. weeksi*. The palpebral lobes of *N. addyensis* are narrower and closer to the glabella and at least partially separated from it by dorsal furrows. *Nevadia cartlandi* (Walcott) differs from the new species in the different position of its eyes.

Horizon.—Lower Cambrian, Addy quartzite, below the pleosponge limestone.

Locality.—Stevens County, Washington, near town of Addy.

Holotype.—No. 1004, Geological Survey of Canada.

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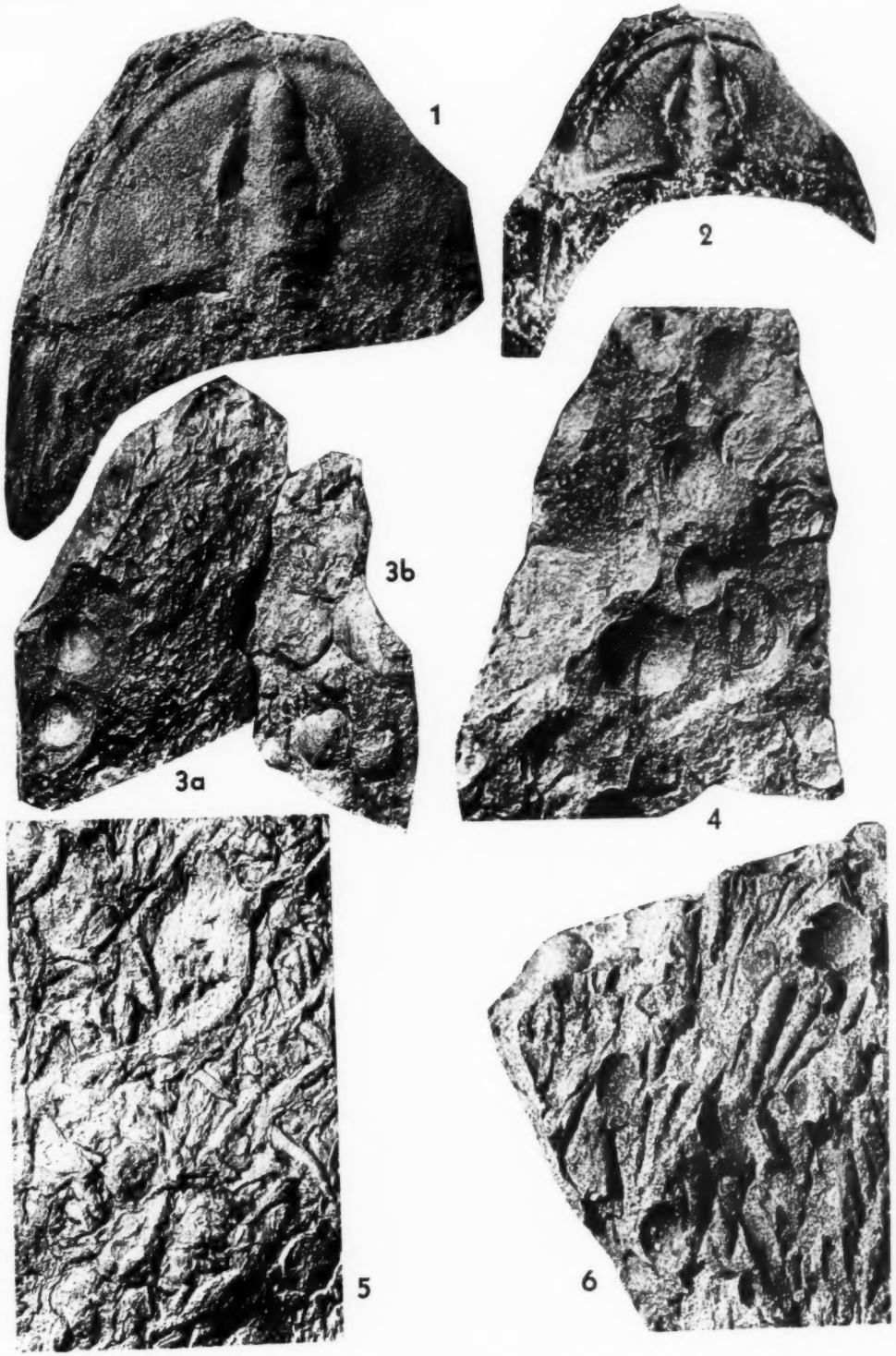
EXPLANATION OF PLATE 62

FIG. *1*—*Nevadia addyensis* n. sp. ×1½. Holotype, No. 10004, Geological Survey of Canada, Ottawa.
2—*Nevadia addyensis* n. sp. ×1. Same specimen photographed in different light to increase contrast.
3a—*Micromitra* sp. ×⅗.
3b—*Kutorgina* cf. *cingulata* (Billings), ×⅗. (Specimen marked 03.)
4—*Rustella* cf. *edsoni* Walcott. ×0.6 and fragments of other brachiopods.
6—Slab of argillaceous Addy quartzite with numerous fucoid imprints. ×½.
7—*Hyolithellus* sp. ×¾. Specimen with a multitude of impressions of *Hyolithellus* and brachiopod impressions.



Okulitch, Washington Lower Cambrian fossils

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JOURNAL OF PALEONTOLOGY, VOL. 25, NO. 3, PP. 408–409, MAY 1951

PALEONTOLOGICAL NOTES

ORDOVICIAN CONODONTS FROM SOUTH AMERICA

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The great majority of conodonts described to date have been derived either from Europe or North America. A few forms (Ordovician) are known from Australia. No specimens appear to have been reported from Asia, and none from Africa except from the extreme northeastern corner, in Egypt. The several "conodonts" recorded previously from South America proved to be scolecodonts. Recently, however, a small collection of Ordovician conodonts was secured by Iglesias from an outcrop at Dique La Cienega (a small water reservoir) about 30 miles south of the City of Jujuy, in the Province of Jujuy, northwestern Argentina. These specimens were sent to Youngquist for study. They all belong to the family Distacodidae, which includes simple cone-shaped forms. The collection consists of only 16 individuals, but at least two genera are represented: *Oistodus* and *Drepanodus*. Judged by these specimens, the containing beds seem clearly referable to the Lower Ordovician. Detailed descriptions and illustrations of the conodonts are being prepared for publication by the Instituto de Geologia y Mineria at Jujuy, a division of the Universidad Nacional de Tucumán, whose main offices are located at Tucumán.

More recently, Iglesias has discovered two other Ordovician conodont assemblages. They came from the Arroyo La Trozada on the northeastern flank of Sierra de Zapla, about 20 miles east of the City of Jujuy; and from the vicinity of the Rio Las Capillas on the northern end of Sierra de Zapla just northeast of the City of Jujuy. These three collections apparently constitute the first authentic and recorded finds of conodonts on the South American continent.

We wish to express our special appreciation to Dr. Juan De Benedetti, Director of the Instituto de Geologia y Mineria, for his interest and aid in this project. The specimens will be deposited in the Institute at Jujuy.

CONCERNING THE SUBSTITUTION OF THE TERM PROSOPON FOR ORNAMENT

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It would be surprising if everyone agreed at first on the proposal of a new term. Wright (Jour. Paleontology, vol. 24, p. 497) questions my proposal to introduce the term prosopon for "the biologically erroneous term ornament" (ibid. 23, p. 572). Two points are raised:

1. It is suggested that a new term is not needed.

Historically, scientific terminology has largely come into being through workers becoming conscious of the inadequacy of terms from everyday speech. An illustration is that of the replacement in recent years of the term reef by bioherm, which in turn is found capable (as an objectively defined term) of qualification and subdivision. In my opinion, prosopon is a parallel example.

2. It is claimed that the new term is objectionable because it is also the name of a genus of Brachyura. However, on procedural grounds this objection cannot be sustained because our rules concerning preoccupation apply only to animal taxonomy. Even the plants have quite an independent system, e.g. *Cymbidium* is both a brachiopod

and an orchid. As Dr. A. Scott Warthin has pointed out, we do not reject the name *Venus* on the grounds that it is preoccupied by a goddess! Moreover, on practical grounds, Wright's own sentence gives the answer to his objection because prosopon is in ordinary type while the genus name is in italics according to standard practice. Also the term has a lower case initial while the genus has a capital initial.

THE NAMING OF FOSSIL FOOTPRINT "SPECIES"*

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For many years fossil footprints have been described in the conventional manner of biologic nomenclature. The custom originated in Europe and was followed by eminent American paleontologists, even though some of them (notably Lull, Gilmore, and Peabody) were fully aware that even a perfect trackway is feeble ground on which to erect a species. Recently, three well known vertebrate paleontologists (Colbert and Schaeffer 1947, Dunkle 1948) raised strong objections to the prevalent custom, on grounds that it violates the basic concepts of zoologic nomenclature, and went on to describe their fossil footprints without referring to them by name.

From a zoological point of view, these objections are justified, although they are "objections of degree and not of kind" (Reeside, personal comment). The propriety of binomial nomenclature for the imprints and casts of shells, for example, never has been questioned. A foot is only a small part of an animal's surface, and correlation of footprints with skeletal remains is rarely practical. A fossil trackway is a uniquely dynamic record of ancient life, but it is not an organism and probably should not be described as such.

The principal reason for naming footprints lies in their possible index value. The footprints "may, in the absence of other fossil criteria, be of considerable value in the correlation of widely separated formations" (Gilmore, 1926). The confusion that would result from nameless index fossils is obvious.

A new system of nomenclature was found useful. The footprint "species" is named by a capital letter and a group of descriptive numbers. A new letter or combination of letters is used for each new "species" described by the writer. Following the letter, the first numeral is to designate the greatest number of feet clearly impressed, and is followed by a decimal point. The numerals after the decimal point refer to the number of clearly impressed toes (if any) on manus and on the pes (in that order). In this way, some degree of ready description is retained in a simple symbol. The numerical part follows established zoologic practice for dental formulae, phalangeal formulae, etc.

For example, a three-toed bipedal trackway of a dinosaur would be named E 2.3, Smith, if the author (Smith) has previously described four other new trackways. The inarticulate pre-Cambrian burrows previously described by the writer (Faul, 1950) are named A 0.0, Faul. Other examples appear elsewhere in this issue.

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NOMENCLATURAL NOTES

NOTES ON NOMENCLATURE OF JURASSIC PHYLLOCERATINA

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My attention has been called to the two following papers:

SORRENTINO, S., 1942, Osservazione su forme e gruppi di ammoniti della famiglia Phylloceratidae Zittel: Riv. ital. paleont., vol. 48, fasc. 3, pp. 1–19.

SORRENTINO, S., 1947, Esame preventivo delle forme assegnate alla famiglia Phylloceratidae Zittel: Boll. Soc. dei Naturalisti, Napoli, vol. 55, pp. 92–97.

In the earlier paper three new generic names are proposed.

Neumayriceras Sorrentino, 1942, p. 14. Type species by original designation *Phylloceras tatricum* (no author mentioned). Assuming *P. tatricum* (Pusch) is meant, this is a subjective synonym of *Calliphylloceras* Spath, 1927. It is also a homonym of *Neumayriceras* Rollier, 1909, a Lower Oxfordian ammonite. In the 1947 paper (p. 93) the spelling *Neumayericeras* is adopted.

Martelliceras Sorrentino, 1942, pp. 14, 15, 17. Type species by original designation "*Rhacophyllites tortisulcatum*" (no author mentioned). Assuming *Ammonites tortisulcatus* d'Orbigny is meant, this is an objective synonym of *Sowerbyceras* Parona and Bonarelli, 1895. It is also a homonym of of *Martelliceras* Schindewolf, 1925 (which is a subjective synonym of *Perisphinctes* Waagen, 1868 sensu stricto), an Upper Oxfordian ammonite. In the 1947 paper (p. 96) the spelling *Martelleiceras* is adopted.

Hyatticeras Sorrentino, 1942, pp. 10. 11. So far as I can see no species is attached to this genus, which is therefore invalid. In any case it is a homonym of *Hyatticeras* Cossman, 1900.

NOTES ON NOMENCLATURE, NOVEMBER 1950

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The first three brochures of the Proceedings of the International Commission on Zoological Nomenclature, meeting in Paris in 1948, were reviewed in the November 1950 issue of this JOURNAL. Four more brochures are now at hand, and volume 4 of the Bulletin of Zoological Nomenclature is now complete except for an index which has still to appear. It seems I was too optimistic about the eventual price of the volume, which now stands at ten pounds, 4 shillings (plus, presumably, another pound or so for the index). This, for some 650 pages of paper-bound letterpress, is almost incredible. I had thought that high printing costs in Britain might be responsible, but I have just on my desk for review a new specialized text put out in Britain, finely printed, well bound, with almost 200 illustrations, which is being sold in Ann Arbor at $4.50, less discounts. Surely the International Trust for Zoological Nomenclature, with the financial assistance of UNESCO, with no dealers' commissions involved, with an advance subscription list, can produce a volume such as this for much less than $30.

This matter is worth harping on, for it is important that the Commission's (or rather the Trust's) publications have a wide distribution. As a working paleontologist, vitally concerned with nomenclature, I would like to have a copy of this Proceedings volume beside me. But at such a price I simply cannot afford it. Nor can I with a straight face recommend to my students that they buy and study it. This is not as it should be.

FIRST REVISER

The Commission decided to change Article 28, to give precise instruction that where two names are published simultaneously for the same taxonomic unit, that which appears first in the original paper is to be used, even though a first reviser has used the second. This summary disposal of the old "page precedence vs. first reviser" controversy is worth examining, since it typifies the kind of procedure which has raised protests in this country.

Although this question is one with wide implications, on which most zoologists have strong opinions, no notice was given that it was to be discussed at Paris. It seems from the Proceedings that the point came up obliquely during discussion of another question (that of determination of priority when two books were published on the same day). The Secretary was instructed to study the problems involved in Article 28, and to submit a report with recommendations. This the Secretary did, between midnight Friday and Monday morning, with time out for a meeting of the Commission on Saturday. His report was presented and considered at the twelfth meeting of the Commission, and we are told that the decision taken was preceded by "a long discussion." This does not sound too bad, if the statement can be taken at face value. Meeting 12 lasted for one hour and fifty minutes. During this 110 minutes 37 separate points were brought up, decisions made and voted on. It is possible that many of these decisions were cursory, taken without time for consideration, although one does not like to think so. But we are told that on five points at least there was "discussion," and on one other than that before us "long discussion." Under the circumstances, I think the reality of any lengthy discussion of this particular point may be doubted. There was here no opportunity for the careful (but time-consuming) weighing of issues which one would expect; no chance for the evocation of after-thoughts which can be so valuable.

This is the more important since, in my opinion, the Secretary's brief was misleading. Much stress was laid on the fact "that a large and increasing number of zoologists ignores the present provisions of Article 28 as applied to a combined species by calling in aid the principle of page preference." What does this mean? If it means that a zoologist acting as first reviser chooses to use the first-printed name, then it has no relevance, since such a zoologist is acting within the limits of the old Article 28, which said only that a first reviser may select any one of simultaneous names, and did not suggest that he should reject the first-printed. The statement quoted would only have relevance if it meant that a large and increasing number of zoologists was ignoring previously selected names, known to them, in favour of rejected first-printed names. This does not seem to be the case. But on this statement rests the Secretary's recommendation that the first-reviser rule be thrown out.

Surely had this matter been discussed fully, some worker would have pointed out that Article 30 (designation of type species) is essentially parallel to Article 28. If the first reviser principle is bad in Article 28, is it still good in Article 30? Apparently so.

Palaeaneilo vs. *Palaeoneilo*

The Commission considered a petition from Dr. L. R. Cox, asking that they use their plenary powers to direct that the pelecypod described by Hall as *Palaeaneilo* be known as *Palaeoneilo*. The name in the form *Palaeaneilo* was used by Hall fifteen times in the original paper, and since this was a preliminary paper which Hall almost certainly saw through the press himself, no question of a lapsus arises. Our Joint Committee sent to the Commission its opinion that the rules should not be suspended in this case.

The Commission ruled that the rules need not be suspended, but that an emendation under the rules should be made, since it was "*évident*" that Hall meant to suggest that his genus was ancestral to the living *Neilo*, and therefore he should have spelled his generic name *Palaeoneilo*. The point involved here is so important that I plan to discuss it at length elsewhere. In the absence of a clear statement in the original paper, how can it ever be "*évident*" that an author meant thus or so? In this case the Commission noted that *Palaeo-* was a common prefix, and deduced that therefore it

was intended here. I think the reverse more probable: *Palaeo-* is a common prefix, well-known to Hall, and if he chose not to use it I would think the choice must have been a deliberate one. There is no evidence in the paper to disprove my own theory, that the prefix was coined as an anagram on the name of Hall's pet spaniel Aleapa, who turned up a fine specimen while chasing a chipmunk.

DESIGNATION OF LECTOTYPE

The Commission has enlarged its powers of interpretation and suspension, so that now it is competent to deal with any type of problem in nomenclature, and to rule on it. One unprecedented ruling should be noted.

An admittedly legal designation of a lectotype from among a group of syntypes has been set aside on the grounds that its recognition would lead to stratigraphic confusion. The species involved is *Ammonites cordatus* Sowerby 1813. During the years since 1813 one of the forms described by Sowerby had become accepted as the typical form of the species, although no formal designation was made. In 1905 another of Sowerby's syntypes was designated as lectotype. The petition for annulment of the 1905 designation, and for a new formal designation of the accepted syntype, was supported by evidence that the species *A. cordatus* (in the accepted sense) was a guide fossil, and had given its name to a zone of the Jurassic. The Commission felt this sufficient reason for suspension of the Règles, and the petition was granted.

MALARIA AND MIGRAINE

Toward the close of its labors the Commission produced what I can only consider a thoroughly woolly piece of legislation. The Commission had been discussing at great length the proper names for human malarial parasites (the summary occupies thirty pages of the Proceedings), had decided on which names should be used, and had invoked plenary powers right and left to settle this very complex question. Fine. But then they decided to issue an Opinion giving post factum legal grounds for one of the decisions they had made.

So we now have a rule saying that, if a specific trivial name is a noun in the genitive case and a subspecific name is proposed with the third term an adjective agreeing with this trivial name rather than with the generic name, then this subspecific trivial name is not to be corrected, but is to be considered completely invalid.

This looks after the particular malarial problem, but what principle are we to take from the opinion? Apparently the only fault lies in the false agreement of the adjective. But why should this not be as faulty if the subspecific name were proposed agreeing in gender with a specific trivial name which was a noun in the nominative in apposition, rather than with the generic name? Are we to take it that any false agreement is ground for rejection of a name? The Opinion does not say so, but confines itself to the particular case of a specific trivial name in the genitive, with no guidance given as to the limits of application. Even interpreted most strictly this Opinion will cause many hours of dusty scurrying for the conscientious, for specific trivial names in the genitive are not rare.

CITATION OF AUTHOR

The new Règles are to contain a provision that, where a description of a new taxonomic unit is clearly stated to be written by an author, then his name is to be cited as author of its name, even though it be published in a work by others. The form of citation is to be " 'B' *in* 'A' & 'B'," or " 'C' *in* 'A'." This accords with much modern practice. Since the purpose of including an author's name is to serve as an abbreviated reference, it should be noted that the latter part of such a citation (i.e. the name or names of the publishing writer or writers) is more important than the first, and should not be omitted. It should also be noted that there must be a clear statement that the mute inglorious author has actually written the description, not just thought of doing it, or not just proposed the name.

WORKS RULED ON

A number of early books and papers were considered and ruled available or unavailable, of which only a few concern us.

The *Tractatus physicus de petrificatis*, by J. Gesner, 1758, is suppressed for nomenclatorial purposes, as are two works by W. Martin: *Figures and Descriptions of Petrifactions collected in Derbyshire* (1793), and *Petrificata Derbiensia, &c.* (1809).

The *Zoologica Fundementa* of Brünnich, 1771, is held to be available. This concerns us only insofar as this work contains a genus *Orthoceros*. The Secretary was instructed to complete consultations with paleontologists as soon as possible on action to be taken with regard to this generic name.

SUSPENSIONS

Among the numerous cases of suspension of the Règles to stabilize usage are a few which concern paleontologists.

The generic name *Graptolithus* Linnaeus 1768, and the specific name *G. scalaris* Linnaeus 1768 are suppressed.

Monograptus Geinitz 1852 is validated by the suppression of *Lomatoceras* Bronn 1834 and *Monoprion* Barrande 1850. The type species is set as *M. priodon* (Bronn), 1834.

Retiolites Barrande 1850 is validated by suppression of *Gladiolites* Barrande 1850. *R. geinitzianus* (Barrande) 1850 is set as type species.

Raphistoma Hall 1847 (type species *R. striata* (Emmons) 1842) is validated by suppression of *Raphistoma* Rafinesque 1815.

The type species of *Trematapsis* Schmidt 1866 is ruled to be *T. schmidti* Rohon 1892, the species actually studied by Schmidt, and not *T. schrenkii* (Pander) 1856, the nominal species designated by Schmidt.

The name *Anomia pecten* Linnaeus 1758 is ruled to refer to the brachiopod currently known as *Strophomena pecten*, in spite of the fact that the name was originally applied to a pelecypod.

The generic name *Pseudoschwagerina* Dunbar & Skinner 1935 is placed on the Official List (type species *P. uddeni* (Beede & Kniker) 1924) thus closing a sorry chapter in nomenclatorial fumbling.

MISCELLANEA

In discussing the ruling that works printed to special purposes, or for special persons, were not "published," I expressed some mild bewilderment concerning the intent of the Commission. A later Opinion now shows that they meant (inter alia?) sales catalogues.

A further ruling was given on homonyms. If two genera have been known by the same name, and the same trivial name has been applied to a species in each, these trivial names are not to be considered homonyms, and the junior need not be replaced.

Any special system of nomenclature devised to assist in referring to fossil fragments would be considered to have no status in zoological nomenclature, and would be no concern of the Commission. This refers to attempts to apply a binomial nomenclature using such terms as "legion," "cohort," etc. It should be noted that the Commission held in another connection, that generic and specific names could be applied under the Règles to the works of animals. Presumably then, names may also be legally given to animals, otherwise unknown, which were responsible for given fragmentary remains. Only if such names are applied to non-zoological units may they be ignored in nomenclature.

Names of sections of genera are to be recognized as subgeneric if they are in classical form in the nominative singular. Specifically, *Aturoidea* Vredenberg is ruled to have standing as a subgeneric name from the date (1925) when it was proposed as the name of a "section" of the genus *Nautilus*.

The old stipulation that a request for suspension of the rules must be advertised for one year in at least two general journals has been changed. Now the period of notice is to be six months, and the publication must be in the BULLETIN OF ZOOLOGICAL NOMENCLATURE and at least one general journal. The main change here seems to be that SCIENCE is published every week, while the volume of the BULLETIN which is devoted to publication of petitions has not appeared for over two years. Now effective notice of a petition cannot be given, and thus consideration of it cannot be secured, except at the pleasure of the Editor of the BULLETIN. The effect of this rule cannot be judged until it is seen in action.

This summary, with the previous notes, covers the points which seem to me of immediate importance to paleontologists in the Proceedings. But the Proceedings are voluminous and wordy, and quite probably on rereading I will see other things which should have been mentioned here.

I cannot close these notes without drawing attention to the extent to which the Commission relied on the advice of our Joint Committee, under the chairmanship of J. Brookes Knight, on questions touching our field. It is obvious from the Proceedings that this advice was very valuable, and valued.

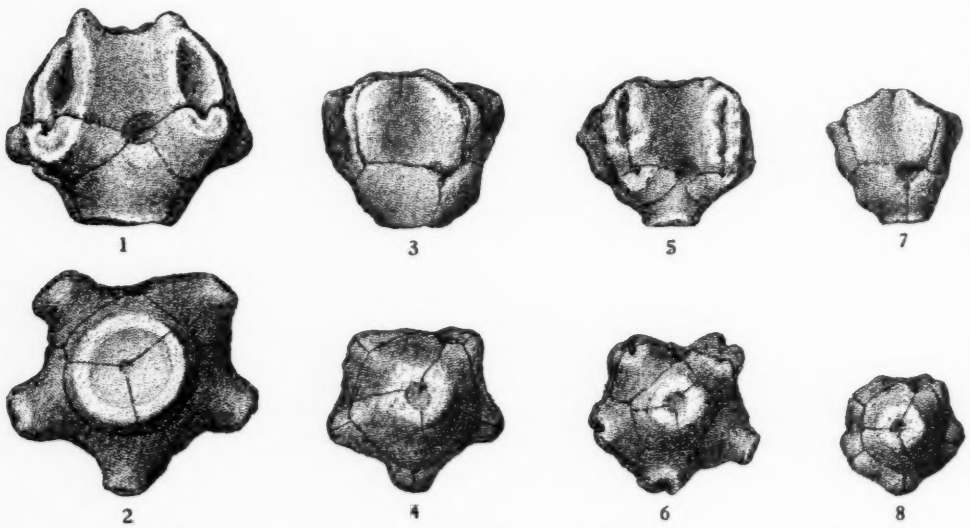
OCTOCRINUS PECK AND *TYTTHOCRINUS* WELLER, SYNONYMS OF *AMPHIPSALIDOCRINUS* WELLER

RAYMOND E. PECK AND JAMES L. CONNELLY, JR.
University of Missouri

ABSTRACT—The micro-crinoid genera *Amphipsalidocrinus* Weller, 1930; *Tytthocrinus* Weller, 1930; and *Octocrinus* Peck, 1936 are combined into the single genus *Amphipsalidocrinus*. After a restudy of the genotype, *Amphipsalidocrinus* is interpreted as monocyclic. Specimens referred to *Tytthocrinus comptus* Weller, 1930 are regarded as immature specimens of *A. scissurus*.

During the course of recent investigations of Kinderhookian and Osagean microcrinoids, an unusually well-preserved specimen of *Octocrinus inconsuetus* Peck (1936) was discovered. This specimen differs from those previously described in the possession of five radial plates bearing attachment areas for arms, and in somewhat larger size (see figure 1). There is no doubt that this specimen represents a mature individual and that the original description of the genus and species was based on immature specimens (Peck, 1936, pp. 291–292, pl. 46, figs. 3–10).

In shape, general appearance, and location of the anal opening, *O. inconsuetus* closely resembles *Amphipsalidocrinus scissurus* J. M. Weller (1930) and *Tytthocrinus comptus* J. M. Weller (1930), both from the Pennsylvanian of Warren County, Indiana. Although Weller (1930, pp. 33–36) interpreted these two genera as dicyclic, his figures 7 and 8 are so nearly like *O. inconsuetus* that physical comparison of types became necessary. Through the courtesy of Dr. H. B. Willman of the Illinois Geological Survey the types of Weller's species were made available to us for study.



FIGS. *1–8*—Posterior and basal views (posterior up) of: *1* and *2*, mature specimen of *Octocrinus inconsuetus* Peck, U. of Mo. E-27-8; *3* and *4*, holotype of *O. inconsuetus* U. of Mo. E-7-1; *5* and *6*, holotype of *Amphipsalidocrinus scissurus* Weller, Ill. Geol. Surv. 46; *7* and *8*, paratype of *Tytthocrinus comptus* Weller, Ill. Geol. Surv. 71. *1–6*, ×27; *7–8*, ×35. (Camera lucida drawings on Ross board by Mrs. Vaona Hedrick Peck.)

Amphipsalidocrinus scissurus is represented by a single specimen, the holotype, and *Tytthocrinus comptus* is represented by the holotype and twenty-four paratypes. The specimens of both species are silicified and suture lines are hard to distinguish.

Weller interpreted the calyx of *A. scissurus* as consisting of an infrabasal disk, five basals, five small radials that do not meet laterally, and an oral dome of five plates. In examining the holotype, the writers noted several features at variance with this interpretation. There are three faint sutures which originate at the center of the stem facet and extend outward. Other faint sutures extend from the proximal edges of the orals toward the stem facet in the interradial position. Neither of these sets of sutures is accounted for in the dicyclic interpretation, but they are in the same position as corresponding sutures in the mature specimen of *Octocrinus inconsuetus*. The writers interpret *A. scissurus* as a monocyclic form with the same calyx plan as *O. inconsuetus*, differing from that species only in size, shape, and general proportions (see figure 1).

According to Weller's interpretation, *Tytthocrinus comptus* possesses an infrabasal disk, five basals, and five orals, with the inter-oral sutures corresponding in position to the interbasal sutures. After close study of the type specimens, we do not agree with this interpretation. Several of the paratypes show three sutures extending outward from the center of the stem facet, and on one of the specimens these sutures extend to the proximal edges of the orals. This is the same type of monocyclic structure displayed by immature specimens of *Octocrinus inconsuetus*, and we believe that *T. comptus* represents an immature stage of *Amphipsalidocrinus scissurus*.

According to our interpretation of the silicified types studied by Weller, *Octocrinus* Peck and *Tytthocrinus* Weller are synonyms of *Amphipsalidocrinus* Weller. With a monocyclic interpretation, *Amphipsalidocrinus* cannot be referred to the Codiacrinidae. We are unable to place *Amphipsalidocrinus* in any defined family of Crinoidea.

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AULACOPHYLLUM SYMMETRICUM, NEW NAME FOR *A. BILATERALE* SLOSS

L. L. SLOSS
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Dr. E. C. Stumm has called my attention to the fact that the name *Aulacophyllum bilaterale* Sloss (Jour. Paleontology, vol. 13, 1939, p. 64, pl. 9, figs. 18–20, text-fig. 5) is preoccupied by *A. bilaterale* Hall (New York State Mus., 35th Ann. Rept., advance sheets, p. 25, 1882; final edition, p. 429, pl. 27, fig. 5, 1884). For the junior homonym I propose the name *A. symmetricum* Sloss, new name.

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